Ecological role of herbivory on coral reefs of the Saudi Arabian Gulf coast

Alistair S. Jolliffe B.Sc. (York)

Thesis submitted for the degree of Doctor of Philosophy

University of Warwick

Ecosystems Analysis and Management Group

Department of Biological Sciences

University of Warwick

Coventry CV4 7AL

United Kingdom

April 1997

Contents

List of Tables

List of Figures

List of Plates

List of Appendices

(Tabulated raw data)

Acknowledgements

As with most undertakings of this nature, especially ones which include travel and work abroad, the number of the people who became involved in, or were affected by this PhD, was considerable. All deserve a personal acknowledgement, but space is limited. Therefore, to all, my thanks and appreciation for services rendered, large or small. Special thanks however, are due to those who played critical roles in helping me successfully complete what originally seemed such a straightforward piece of research. Therefore, and in no particular order, I would like to thank the following for all their efforts:

Andrew Price for his support, enthusiasm and guidance, while steadfastly playing the unenviable role of supervisor.

Lionel Jolliffe for assisting in the purchase of materials and guidance in the construction of the exclusion cages.

Mubarak Al-Marri for collecting yet more urchins from Abu Ali and to Friedhelm Krupp for carrying them all the way back to Europe in his hand-luggage.

Phil Basson for double-checking the identifications of the algae from the reference collection.

John Marshall for his help and patience with all those infuriating computer problems, especially when my own computer decided to expire. Also the use of his computer and office during the final stages of writing-up.

Axel Plaga, Rod Fleming, and Jaime Plaza for providing boat and dive support, the majority of which was given during their spare time.

James Cole for driving me all the way to Stoke-on-Trent in the Department's minibus to collect the settlement plates.

Ahmed Salah for helping me shop for building materials to make the concrete blocks and getting them out to Abu Ali.

Torres and Samman for cooking for me for a year.

Ruth and Jeremy Thorpe, Rebecca Klaus, James Cole, and Susan Taylor for providing a place to stay when I've needed one.

Keith Longman for providing the large supply of cable-ties free of charge.

Peter Symens for allowing me to assist him during his ornithological work as 'light' relief from my own, and the opportunity to experience the contrasting regions of Saudi Arabia.

Pascale Symens for unlimited use of her tapes, CDs and portable stereo throughout those long hours in the dry lab.

Finally, very special thanks go to my parents for keeping me well fed and watered when things took a little longer than expected, but most importantly to Friedhelm Krupp for supporting this research by allowing unlimited access to all facilities of the Jubail Marine Wildlife Sanctuary for an entire year. Without it, this PhD would have probably remained nothing but a nice idea.

Declaration

This thesis is the result of original research conducted by myself, unless stated otherwise in the text, under the supervision of Dr ARG Price. All sources of information have been specifically acknowledged.

No part of this work has been submitted for a degree at any other University.

Alistair Jolliffe, April 1997

Summary

This study examined the ecological role of herbivory on coral reefs of the Saudi Arabian Gulf coast. Herbivory is a ubiquitous process and important in regulating benthic marine communities. Three reef sites were studied over a 12-month period; one on an inshore fringing reef (1.5 m depth), and two on the fringing reef surrounding an offshore island (3 m and 11 m depth). The inshore site experienced greatest extremes in temperature, salinity and sedimentation.

The ecological role of herbivory was determined from algal settlement plates and their selective exclusion from herbivores. The inshore site was naturally dominated by filamentous algae, while both offshore sites supported a higher proportion of crustose forms. Location (i.e. distance from shore) appeared to be more important than seasonality in determining the structure and composition of the epilithic algal community. At the inshore site herbivorous fish (dominated by *Siganus* spp.) imposed a uniform, wide-ranging grazing pressure of intermediate intensity. Herbivorous echinoids (*Echinometra mathaei*) imposed an intensive but localised grazing pressure. At the shallow offshore site, only herbivorous fish (dominated by *Scarus* sp.) appeared responsible for grazing impacts, which were also intensive. At the deep offshore site both herbivorous fish (dominated by *Pomacentrus* spp.) and echinoids (*Diadema setosum*) were responsible for limiting algal growth, although other factors (e.g. light penetration) may also inhibit algal productivity at this site. An experiment assessing the effects of extreme perturbations (i.e. removal of the algal community), showed that seasonal life-history strongly affected generic succession and rate of re-colonisation. Perturbation effects were temporary and did not precipitate permanent alternative stable communities.

An important secondary effect of herbivory is bioerosion. The mean erosion rate by *E. mathaei* was comparable to rates recorded elsewhere. Behavioural studies revealed that burrow defence and fidelity were positively correlated with burrow complexity, and that the frequency of agonistic behaviour was low. Foraging range was negatively correlated with burrow complexity. In addition, the risk of mortality by finfish predators at the inshore site was estimated to be very low.

The study has shown that Saudi Arabian Gulf reef communities may be particularly vulnerable to the depletion of herbivores, for example by overfishing. Management plans should therefore safeguard the herbivorous community, in order to maintain natural bioerosion rates and other reef processes.

SECTION ONE

Introduction

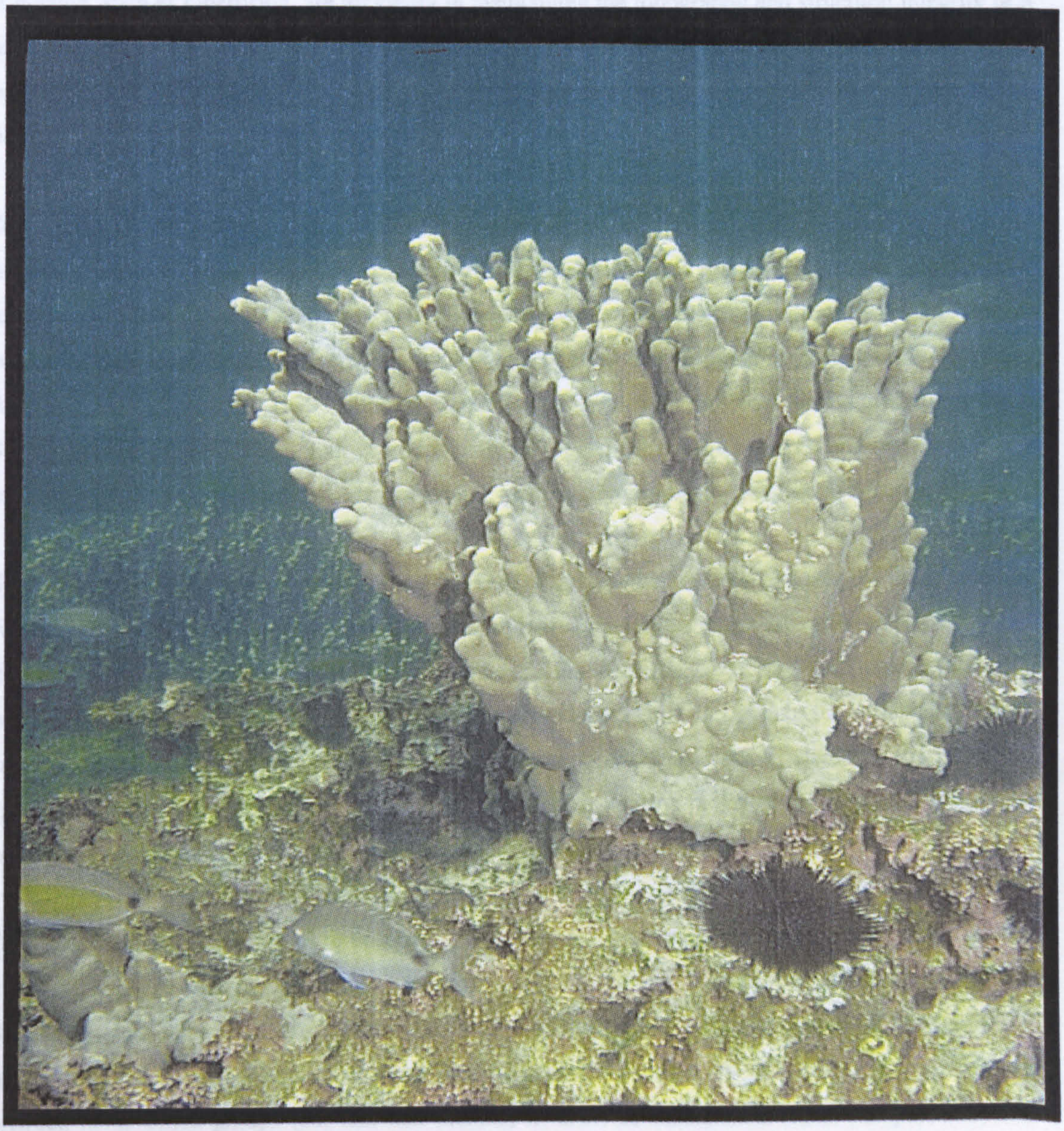


Plate 1.0: A colony of *Porites* sp., the dominant genus of hermatypic coral found at Abu Ali and other inshore reefs along the Saudi Arabian Gulf coast (8/94).

Chapter One

General Introduction

On most coral reefs the abundance of the benthic algal community is low and characterised by a mixed assemblage of filamentous and crustose coralline algal forms interspersed with developing macroalgae (Steneck, 1988). This feature of reefs has been mainly attributed to the ubiquitous process of herbivorous grazing, which is particularly intense in shallow, wave-exposed reef habitats (Hixon, 1983; Steneck, 1988). Herbivory is an extensively studied area of coral reef ecology, and its importance in regulating the composition, structure and productivity of the benthic algal community is well-documented (reviewed by Hatcher, 1983; Steneck, 1988; Glynn, 1990). Furthermore secondary effects of grazing, such as bioerosion, are important in maintaining the topography and structural integrity of a coral reef (Hutchings, 1986; Glynn, 1996). Geographically however, research has centered mainly on the Pacific and Caribbean regions, whereas very few studies have been undertaken in the wider Indian Ocean.

Coral reefs of the Arabian Gulf, unlike those investigated in the majority of studies, exist at the latitudinal limits of their tolerance, and as a result are characterised by seasonally-stressed, species-poor communities, although abundances are often high (Sheppard *et al.*, 1992). Environmental conditions in the Gulf are some of the most severe experienced by any coral reef community in the world (Coles and Fadlallah, 1991; Sheppard, 1993), although depth and distance from the coast have a mediating effect. Due to their relative isolation, both geographically and logistically, little research had been conducted until recently on the coral reef habitats of the Gulf, particularly concerning the role of herbivory.

Given the extreme conditions prevailing in the Gulf, it is hypothesised that the relative importance of the processes and species that structure and regulate reef communities might differ from those observed for coral reefs found in more equable environments. For example, herbivory may have a relatively minor role in controlling the abundance of benthic algae in the Gulf, throughout the seasonal cycle, or just during particular seasons. Conversely, if herbivory was important in stressed, low diversity communities then the presence of a particular herbivorous species or group may be relatively more important in maintaining community structure than in ecosystems of higher diversity.

The main aim of this study was to compare the relative importance of herbivory on the structure and composition of the benthic algal community growing on inshore and offshore reefs of the Saudi Arabian Gulf coast, and its implications for the coral reef communities. The study continued throughout an entire 12-month, seasonal cycle and examined the process of herbivory at two levels: intrinsically between herbivorous groups (i.e. fish and urchins) in order to assess their relative importance; and extrinsically between the process of herbivory and the seasonally extreme environmental conditions which characterise the Gulf marine ecosystem. An additional aim was to investigate the ecological

consequence of a secondary effect of grazing, that of bioerosion, particularly by urchins, and its relative influence on coral reef topography and integrity.

Following the general introduction (Chapter 1), the thesis begins by an examination and interpretation of the current literature and status of knowledge regarding the process and importance of herbivory, its secondary bioerosive effects and the marine ecosystems of the Arabian Gulf (Chapter 2). Three ecologically different reef sites were used as the study areas for the present research work (Chapter 3). Firstly, in order to examine the effect of distance from the mainland shore, one study site was located on a shallow inshore reef, and the other on a correspondingly shallow offshore reef. Secondly, in order to examine the effect of depth, the third site was located on a deep offshore reef. The effects of the extreme environmental conditions on marine communities of the Gulf are well known, and therefore the seasonal fluctuations of water temperature, salinity and sedimentation were monitored at each of the reef sites throughout the study period (Chapter 4).

Settlement plates were established at each of the study sites, in order to simulate the natural substratum under normal grazing conditions. The plates were sequentially sampled throughout the study period in order to monitor and compare seasonal changes in generic composition and structure of the respective epilithic algal communities (Chapter 5). Selective exclusion cages were also deployed over some of the settlement plates, in order to isolate the impacts of different herbivore groups (i.e. fish and urchins). The status of the affected algal communities was then monitored over time (Chapter 6). In addition, the effects of extreme perturbations on the pattern and rate of succession of the algal community were also investigated at the inshore site (Chapter 7). The work in Chapters 5 and 6 was complemented by observations on the composition and densities of herbivorous communities at each of the reef sites throughout the study period (Chapter 8).

Erosion of reef material is an important secondary effect of the grazing activities of herbivores (i.e. urchins), particularly if erosion rates exceed reef accretion rates. This is especially relevant to Gulf reefs, as the stressful environmental conditions inhibit reef growth in many areas. Therefore the bioerosive impact of grazing urchins was investigated throughout the diel period and compared between seasons (Chapter 9). This was augmented by studies on the diurnal feeding behaviour of urchins (Chapter 10).

The research was concluded by a review of the research approach adopted, and an assessment of the role of herbivory on coral reefs of the Saudi Arabian Gulf coast (Chapter 11). The implication of the results to management was also discussed.

Chapter Two

Reviews of Herbivory, Bioerosion and the Arabian Gulf

2.1 Herbivorous grazing on coral reefs

The process of herbivory is a common phenomenon throughout many ecosystems and is one of the most intensively studied areas in coral reef science (reviewed by Hatcher, 1983; Steneck, 1988; Glynn, 1990). Researchers have also focused on the relative impact and role of grazing by different taxonomic groups, such as fish (reviewed by Ogden and Lobel, 1978; Hixon, 1983; Horn, 1989; Hixon, 1997), and invertebrates (reviewed Ogden and Lobel, 1978; Brawley and Adey, 1981; Lawrence and Sammarco, 1982; Carpenter, 1997). Several decades ago early workers first demonstrated how the low biomass of benthic algae, a characteristic of coral reef substrata, is maintained through the intensity of the grazing pressure exerted by the herbivore community (Hiatt and Strasburg, 1960; Stephenson and Searles, 1960; Randall, 1961). Since these pioneering studies, research has continued to explore the mechanisms and patterns behind the herbivory process and their relative importance in regulating the structure, composition and productivity of benthic algal communities.

2.1.1 Benthic marine algae

Throughout the coral reef ecosystem, algal species can be found performing a variety of essential roles (see Borowitzka, 1981). However the group responsible for the majority of primary productivity in the reef system is the non-symbiotic benthic algae (Larkum, 1983; Adey and Steneck, 1985; Hatcher, 1988). This diverse group of species can be divided into a number of categories, determined by various anatomical and morphological characteristics (Steneck, 1988; see Table 2.1). This functional group approach facilitates the isolation of general trends in algal community composition (Steneck and Dethier, 1994). On coral reefs, most patches of dead calcium carbonate substrate are dominated by a low standing crop of fast-growing algae. Termed as the epilithic algal community (EAC), this species rich community is characterised by aggregates of small filamentous and fleshy algae, with occasional macroalgae and areas of crustose coralline algae. The components of the EAC, particularly the filamentous 'turf' algae, have been identified as the most important sources of primary production entering the coral reef ecosystem (Larkum, 1983).

2.1.2 Herbivore community

The herbivore community is composed of a diverse range of species from many different phyla, and constitutes an important part of the reef fauna (Carpenter, 1997; Hixon, 1997). Considering reef fishes alone, it has been estimated that up to 35% of the species diversity and biomass is attributable to herbivorous fishes (Ogden and Lobel, 1978; Sutton 1983).

Differential preferences and grazing intensity

In order to reveal any differential algal preferences amongst this diverse community of reef herbivores, researchers have employed a variety of techniques. For example, gut analyses have been used to reveal food preferences and determine whether a particular herbivore is a specialist or generalist feeder. Amongst herbivorous fish, studies have revealed the existence of differential feeding patterns within and between taxonomic families (Nelson and Chiang, 1992; Ochavillo *et al.* 1992; Polunin *et al.* 1995). In their review, Russ and St. John (1988) summarised data from 91 species of herbivorous fish which revealed clear preferences in food items between taxonomic families (Table 2.2). Overall, the epilithic algal 'turf' is the most preferred form, although most groups also consume a proportion of detritus and inorganic material, particularly parrotfish. In contrast, the majority of echinoid grazers are generalist feeders although most show avoidance behaviour towards unpalatable algal forms (reviewed by de Ridder and Lawrence, 1982).

Feeding rates have been the most commonly used approach to estimate the grazing intensity of a particular herbivore. In the case of reef fish this has been directly quantified by counting the number of bites taken over time, either by personal observation (Morrison, 1988) or time-lapse photography (Steneck, 1983; Carpenter, 1986). An indirect measure used for both fish and urchins was the bioassay technique, whereby strips of palatable algae (i.e. *Thalassia*, *Acanthophora* and *Gracilaria* spp.) of known size and weight were attached to the substratum throughout the reef (Hay, 1981a; Nelson and Tsutsui, 1981; Steneck, 1983; Lewis, 1986). The comparative amount of algal biomass removed by grazers was considered indicative of the grazing pressure across different reef zones. However, Hay (1984a) cautions against extensive use of the bioassay technique, as it only considers the combined impact of fish and urchin grazers and ignores microherbivores and other invertebrate herbivores. In addition it is predisposed towards predators that respond to visual cues (i.e. fish).

The size of foraging ranges have also been used as a measure of grazing intensity. In fish this is mainly influenced by territorial behaviour. For example, most strongly territorial pomacentrids are restricted to small areas (Ogden and Lobel, 1978) while large schools of parrotfish cover large areas of reef, although they tend to have preferred feeding areas (Horn, 1989). Foraging ranges have also been measured for some grazing echinoids (Carpenter, 1984).

Functional groups

Unfortunately it is impractical to attempt to quantify the role of every grazing species. Instead researchers have attempted to simplify the complexity of the interactions within the community by organising the herbivores into functional groups (Carpenter, 1983; Steneck and Watling, 1982; Steneck, 1983, 1988). As with the algal community these categories are based on morphological and ecological characteristics. For example, Carpenter (1983) selected herbivores according to their foraging ranges and grazing frequency (Table 2.3a). A similar and more generally accepted classification is described by Steneck (1988) where the functional categories are defined by the effectiveness of grazing types of algae and the impact on the substratum (Tale 2.3b). Such forms of classification have facilitated investigations of the differential effects that different groups of herbivores impose upon the algal community structure, biomass and primary productivity (see below).

However, while this approach provides analytical convenience it assumes a uniform level of impact within functional groups. Small but potentially profound differences exist between functional conspecifics. For example, in terms of behaviour and physiology, Montgomery *et al.* (1989) discovered important differences between three species of surgeonfish which influenced their relative impact on the benthic algal community. More interesting are the recently discovered morphological differences in the mouthparts of parrotfish (Bellwood and Choat, 1990) and surgeonfish species (Purcell and Bellwood, 1993), and consequently their feeding mechanisms. Hence differential grazing effects on the benthic algae also occur at the mesoscale. Choat (1991) stresses caution when analysing functional group-based results as any variations between members of a group will be magnified by differing densities within communities.

Patterns of herbivory

Studies of spatial patterns have shown that herbivory is most intense at shallow depths, below the wave-base on the reef crest and shallow forereef, and declines linearly with depth along the reef slope (Hay, 1981a; Hay and Goertemiller, 1983; Hay *et al.*, 1983). Reduced herbivory is also found on shallow algal ridges and backreef areas (Steneck, 1983; Hay *et al.*, 1983). Hence for a typical windward coral reef, the general pattern of bathymetric grazing intensity is unimodal in distribution (Hixon, 1983; see Figure 1 in Steneck, 1988).

Furthermore, studies have examined differential patterns in herbivore community composition and therefore the relative importance of different herbivorous taxonomic groups responsible for these spatial patterns of grazing intensity. For example on Jamaican forereefs, Morrison (1988) discovered that while the grazing echinoid *Diadema antillarum* was the dominant herbivore in shallow areas, it played a minor role relative to herbivorous fish (mainly scarids) in deeper areas. Similarly between taxonomic families, Lewis and Wainwright (1985) revealed that while scarids were the predominant

herbivorous fish on deeper reef areas, acanthurids dominated the shallow reef habitats. However, Hay (1984a) points out that on Caribbean reefs in particular, the dominant or equal grazing intensity by echinoids relative to herbivorous fish, that also increases with depth, is characteristic of overfished reefs. Conversely, a dominance by herbivorous fish, low echinoid abundance and a grazing intensity that decreases with depth, is indicative of an unfished reef. Hence in some areas the observed patterns of herbivory may also be reflective of the local fishing pressure or other harvesting practices (but see Hixon, 1985).

Reduced herbivore distribution and grazing intensity is usually due to limiting factors such as strong wave action (Russo, 1977; Foster, 1987; Muthiga and McClanahan, 1987, Dotan, 1990), the absence of refuges from predators (Hay, 1981a; Lewis and Wainwright 1985; Lewis, 1986; Muthiga and McClanahan, 1987) and population decline, either from removal (i.e. overfishing Hay, 1984a; Sammarco, 1982b) or increased natural mortality (Lessios, 1988a). Herbivore grazing intensity can also be restricted within habitats by biological interactions. For example, Levitan and Genovese (1989) showed that predation pressure limits the distribution and foraging behaviour of *D. antillarum* to reef habitats with suitable refuges. Some damselfish (i.e. *Stegastes*, *Eupomacentrus*, *Hemiglyphidon*) and surgeonfish (i.e. *Acanthurus sohal*) aggressively defend territories of cultivated algal turf and prevent or inhibit the foraging activities of grazing echinoids (Sammarco and Williams, 1982; Robinson and Williams, 1985; Eakin, 1988), and herbivorous fish (Vine, 1974; Sammarco and Carleton, 1981). However, Williams (1981) revealed that such inhibitory behaviour can also indirectly enhance herbivore diversity. In this case by mediating the competitive interactions between two echinoid species.

Temporal patterns in herbivory also exist. For example, all herbivorous fish are diurnal feeders whose peak activity occurs during the morning and declines in the afternoon until reaching the lowest rates that occur throughout the night (Hay *et al.*, 1983). Furthermore on a seasonal basis, Hatcher (1981) showed that grazing rates and gut turnovers of herbivorous fish were markedly seasonal and correlated with temperature (i.e. declined three-fold during the winter).

2.1.3 Effects on the benthic algal community

Distribution and biomass

The majority of coral reef habitats are characterised by a low standing crop of benthic algae (Hatcher, 1983; Steneck, 1988; Scott and Russ, 1987), which correlate with those areas experiencing intense grazing pressure by herbivores (Klumpp and McKinnon, 1992; see above). It is now undisputed that the presence of herbivores reduces algal biomass and their exclusion or removal allows the algal community to flourish (Hay and Taylor, 1985; Steneck, 1988). Natural examples of herbivores limiting algal biomass were observed by Randall (1965) and Ogden *et al.* (1973) through the formation of

haloes of bare substratum around patch reefs situated within seagrass beds that were formed by the grazing activities of herbivores foraging from the reef refuge. The early experimental studies by Stephenson and Searles (1960) and Randall (1961) further showed how the artificial exclusion of herbivores from the substratum was followed by an increase in algal biomass. This basic principle of manipulative exclusion was been employed by numerous studies investigating the effects of herbivory (Sammarco *et al.*, 1974; Hatcher, 1981; Sammarco, 1982a; Sammarco and Carleton, 1981; Hatcher and Larkum, 1983; Sammarco, 1983; Carpenter, 1986; Lewis, 1986; Scott and Russ, 1987; Morrison, 1988; Hixon and Brostoff, 1996).

These and other studies have illustrated the extent to which herbivores are able to regulate the distribution and biomass or standing crop of benthic algae. For example at large spatial scales, such as between reef habitats, Scott and Russ (1987) revealed that across the Great Barrier Reef, Australia, grazers had a greater impact on epilithic algal composition and biomass on mid- and offshore reefs, than inshore reefs. Furthermore these conclusions correlated with distribution of the herbivorous fish measured across the Great Barrier Reef (Russ, 1984a,b). Within reef habitat studies, such as those by Hay (1981a,b), have shown that herbivores are able to restrict macroalgae to areas where herbivores do not occur. For example, algal species found on the reef flat and sand plain areas were effectively excluded from the reef slope (Hay, 1981a; Hay *et al.*, 1983).

The correlation between grazing pressure and algal distribution and biomass is well known (Steneck, 1988; Klumpp and McKinnon, 1992). Lewis (1986) demonstrated that herbivorous fish were capable of maintaining a herbivore-tolerant algal turf assemblage. Similarly with grazing echinoids, Carpenter (1981) and Sammarco (1982a) revealed that algal biomass decreased with increasing urchin density and grazing pressure. A further avenue of research has also been to examine the differential impacts and relative importance of taxonomic groups (i.e. urchins and fish), by observing the shifts in community composition, biomass and productivity under different grazing regimes (Carpenter, 1983, 1986; Morrison, 1988).

In contrast, however, the grazing activities of a minority of herbivores can actually increase algal biomass. Territorial damselfish cultivate areas of predominantly filamentous algae by imposing an intermediate grazing pressure (pomacentrids are classified as non-denuding, Steneck, 1988; Table 2.3b), and by aggressively excluding other herbivores (Brawley and Adey, 1977; Lobel, 1980; Montgomery, 1980; Hixon and Brostoff, 1981). In fact herbivorous damselfish are important contributors to the overall distribution and biomass of benthic algae within reef habitats, as it has been estimated that the coverage of their territories can range from 15-50 % of the reef substratum (Sammarco and Carleton, 1981; Sammarco and Williams, 1982).

Hence herbivores are able to limit the distribution and regulate the biomass and composition of the epilithic algal community. However, Hatcher and Larkum (1983) caution against the assumption that

herbivory is entirely responsible for, and an adequate predictor of, benthic algal standing crop. Their study on the Great Barrier Reef, Australia, showed that in shallow and intertidal areas, algal biomass was three to five times higher than in deeper areas, despite a high yield to grazers. Furthermore on outer reef slopes, inorganic nitrogen levels limited productivity even though the standing crop was determined by losses from grazers. Foster (1987) recorded three times more algal biomass on exposed areas where urchin grazers were excluded, due to wave surge. Hence while herbivores place a lower limit on the rate of productivity the algal community must support to survive, other factors (i.e. nutrient levels and light intensity; see below), will impose an upper limit. Therefore when grazing intensity does not equate to the observed standing crop, other factors must be contributing to the spatial and temporal patterns.

Community structure and diversity

The standing crop or biomass of an algal community is ultimately indicative of the current balance between its rate of biomass production and rate of biomass removal, (Steneck, 1988; Steneck and Dethier, 1994). However, various studies have also demonstrated that changes in disturbance or rates of biomass removal, such as grazing intensity cause shifts in the composition and structure of the benthic algal community (Carpenter, 1986; Lewis, 1986; Liddell and Ohlhorst, 1986; Scott and Russ, 1987; Morrison, 1988). Such shifts are a function of the susceptibility of the algal thallus to grazing pressure. For example, fleshy, delicate macrophytes will only thrive in areas of low grazing pressure, while under high levels of disturbances only the most resistant forms will be able to survive, such as crustose corallines. Therefore under increasing grazing intensity the gross shifts in community composition range from macrophyte - filamentous - crustose forms (see Figure 2 in Steneck, 1988), and at even higher grazing pressures, only cyanophytes survive (Miller, 1982; Sammarco, 1983; Wilkinson and Sammarco, 1983).

Studies have also investigated the impact of herbivory on algal diversity. Hay (1981b) illustrated how between-habitat diversity will be maintained through variable grazing intensity across reef habitats, due to patterns of herbivore distribution. Within-habitat diversity is also dependent upon the level of grazing intensity exerted. Connell (1978) argued that diversity should be maximised under intermediate grazing pressure. Termed as the Intermediate Disturbance Hypothesis it proposed that at the highest levels of herbivory algae will be ultimately excluded, and at the lowest levels successional interactions will result in competitively superior taxa dominating the community. Researchers tested this hypothesis by examining the compositions of algal communities under different grazing regimes (Carpenter, 1981; Hixon and Brostoff, 1981;1983; Sammarco, 1983; Hixon and Brostoff, 1996). In accordance with the hypothesis these studies demonstrated that community diversity can be maximised under intermediate grazing pressure. Furthermore Hixon and Brostoff (1981;1983;1996) revealed that this was due to herbivorous grazing effectively altering the successional trajectory of the algal community. At the highest levels of disturbance (i.e. outside damselfish territories), grazing impacts the successional

process at its earliest stages, allowing only prostrate and crustose forms to exist. At intermediate levels (i.e. inside damselfish territories), grazing suspends the community at intermediate stages of succession, while at low levels (i.e. inside exclusion cages), ungrazed communities initially support the highest diversity until competitive exclusion resulted in the community being dominated by one or two genera. Hixon and Brostoff (1983) point out that the damselfish was effectively a keystone predator in reverse (*sensu* Paine, 1966), whereby a reduction in grazing pressure increases community diversity.

However the intermediate disturbance hypothesis does not always hold. Sammarco (1982a) found that as echinoid grazing pressure (i.e. density) increased, algal diversity exponentially decreased. The reason for this result was the absence of a competitively dominant species, without which diversity will not be reduced under the lowest levels of grazing (Yodzis, 1976). Hence as Sammarco (1982a) points out, the initial composition prior to changes in grazing pressure, and the recruitment of a competitively dominant alga, are critical in determining the resultant composition of the community.

The selective effects of grazing has also resulted in the evolution of specific algal defences to deter herbivores, such as secondary chemicals and mineral or fibrous skeletal materials (Hay and Goertemiller, 1983; Littler *et al.*, 1983; Hay, 1984b; Duffy and Paul, 1992; Hay *et al.*, 1994).

Productivity

Benthic algae, particularly the filamentous 'turf' algae, are the most important contributors to the overall primary productivity of the coral reef community (Hatcher, 1988; 1990), but their rate of photosynthetic production is dependent on various limiting factors. The most important are; light intensity, temperature, nutrient supply, inorganic carbon supply, oxygen concentration and circulation (Larkum, 1983). The latter is important for ensuring the continuous diffusion of metabolites to and from the water column and the algal tissues. Due to the mechanics of fluid dynamics and boundary effects, the faster the flow rate (that is preferably oscillatory in nature), and the lower the projection of the algal thallus above the substratum (i.e. reduced boundary layer), then the higher the rate of metabolite diffusion and exchange (Carpenter *et al.*, 1991; Carpenter and Williams, 1993).

Despite the reduction in algal biomass and damage to photosynthetic tissues that grazing imposes, the activities of herbivores actually enhance the productivity of the benthic algal community (Wilkinson and Sammarco, 1983; Klumpp *et al.*, 1987; Klumpp and McKinnon, 1989). Studies have shown that despite a reduction in standing crop, areal productivity remains comparable (Carpenter, 1986; Klumpp and McKinnon; 1992). Firstly grazing selectively removes larger macrophytes with lower specific productivity rates and secondly maintains the thalli of the remaining taxa at their most rapid growing phase (Larkum, 1983; Hatcher, 1983). In addition, the effect of reducing algal biomass and therefore standing crop height further enhances productivity through the reduction of the boundary layer and its associated inhibitory effects on metabolite diffusion. Productivity may also be further enhanced by the

excreta of herbivore metabolism, and so provide an additional source of nitrogen through ammonium products (Williams and Carpenter, 1988). Grazing also restricts the accumulation of sediment within dense algal stands which can subsequently inhibit productivity through the development of anoxic conditions (Sammarco, 1983; Sammarco and Carleton, 1981). However algal primary productivity is only maximised at intermediate grazing pressures (Brawley and Adey, 1977; Carpenter, 1981; Klumpp *et al.*, 1987).

2.1.4 Role of herbivory

The ubiquitous process of herbivory and its associated effects are probably the most important regulators of the reef community structure and integrity (Hatcher, 1983). Its primary role is the rapid assimilation of plant material, the production of secondary metabolites and therefore energetic transport and dispersal of the algal primary productivity throughout the trophic levels of the reef community (Klumpp and Polunin, 1989). This process is enhanced by the selective grazing activities that maintain the benthic algal community in its most productive composition and growth phases. Patterns of herbivory also maintain algal diversity within and between reef habitats.

The maintenance of a low standing crop also has important secondary effects. Without the continuous reduction of algal biomass, other sessile organisms, such as corals and sponges, would be competitively excluded by the superior, fast-growing algae (Ogden and Lobel, 1978; Hughes *et al.*, 1987; Carpenter, 1988; Levitan, 1988c). Hence loss of the grazing herbivores would have severe implications for the overall reef community structure. The mass mortality of the grazing echinoid, *D. antillarum* and the subsequent changes in the benthic communities is now a classic example. In 1983, starting in Panama and spreading throughout the Caribbean (Lessios *et al.*, 1984a), a water-borne pathogen caused widespread mortality of the long-spined urchin (Lessios, 1988a). For example, in the San Blas Archipelago 95-99% mortality occurred (Lessios *et al.*, 1984b), while 98-100% was recorded in Curaçao (Bak *et al.*, 1984) and close to 100% on Jamaican reefs (Hughes *et al.*, 1985). Hence across the reefs of the Caribbean the average level of mortality was greater than 93% of the resident populations (Lessios, 1988a). Furthermore, when recovery to pre-mortality levels of abundance was not forthcoming, it was suspected that population densities were now too small to ensure widespread recruitment (Lessios, 1988b). Only on the reefs around Barbados did significant recruitment occur (Hunte and Yungalo, 1988). This was primarily due to the presence of populations that were approximately one magnitude larger than others across the Caribbean (Lessios, 1988a), despite experiencing similar levels of mortality (Hunte *et al.*, 1986).

Studies had previously shown the echinoid to be an important herbivore in the many reef ecosystems on which it occurred (Ogden *et al.*, 1973; Carpenter, 1981; Lewis and Wainwright, 1985) and as such, was a critical agent in limiting the growth and distribution of benthic algae, particularly the filamentous and fleshy macroalgal forms (Sammarco, 1982a; Carpenter, 1983, 1986; Morrison, 1988). Consequently,

the widespread depletion of herbivore abundance resulted in a massive reduction in grazing pressure and a release from herbivory for the benthic communities. As predicted, the demise of *D. antillarum* heralded a rapid increase in algal biomass (Liddell and Ohlhorst, 1986; de Ruyter van Steveninck and Bak, 1986; Hughes *et al.*, 1987; Carpenter, 1988; Levitan, 1988c). Not only did this reduce further recruitment of other sessile organisms, such as corals, but also increase the mortality of resident taxa, such as coralline algae, through shading and sediment accumulation (Hughes *et al.*, 1987). These benthic and community changes had important implications for the process of trophic transport of productivity throughout the reef ecosystem (Carpenter, 1988). Without sufficient grazing intensity to harvest and maintain a low standing crop, benthic algae were developing mature thalli. These macrophytes then began to dominate the substratum, and were subsequently washed from the reef. This productivity was therefore being lost to the reef ecosystem (Carpenter, 1990a). The loss of the echinoid further impacted over reef inhabitants to the extent that fish predators of the urchin had to alter their diet, becoming predominantly generalist feeders instead (Reinthal *et al.*, 1984; Robertson, 1987). Studies had also shown that removals of competitively dominant *D. antillarum* were followed by increased densities of other herbivores (Hay and Taylor, 1985). It was therefore hoped that other herbivorous groups, such parrotfish and surgeonfish, would increase in numbers and fulfil the grazing role vacated by *D. antillarum.* Unfortunately, despite observed increases it does not seem to be sufficient to return the reef community to pre-mortality conditions (Carpenter, 1990b; Robertson, 1991), possibly due to over-fishing effects (Hay, 1984a). Hence the example of the mass mortality of *D. antillarum* clearly demonstrates the importance of herbivory in regulating the competitive balance between sessile organisms and maintaining the reef community structure.

The other major secondary effect of herbivory is the excavation of reef material. Termed *bioerosion* (see section 2.2), physical abrasion of the substratum by the more dominant grazers, such as urchins and parrotfish, results in its exposure and subsequently facilitates the recruitment, colonisation and distribution of sessile organisms such as corals (Dart, 1972; Sammarco, 1980; 1982b; Birkeland and Randall, 1981). The bioerosive activities of herbivores also sculpt and modify the reef framework into a heterogeneous, multi-habitat structure (Hutchings, 1986; Glynn, 1997). However such impacts need to be balanced with constructive processes or else reef degradation can occur (see section 2.2). Therefore in accordance with the loss of herbivores, an excess is also detrimental to the overall health of the reef.

2.2 Bioerosion on coral reefs

The complex morphology of both modern and ancient reefs is the result of a balance between opposing forces. Constructive processes known collectively as *reef accretion* involve the deposition of organic and inorganic material which forms the reef, while destructive forces or *reef erosion*, erodes and sculpts the reef material. The combination of these two processes controls the overall *reef growth.* However as Trudgill (1983) points out, reef growth is not a uniform or static process, but an interaction between

variable factors. For example, material may be eroded from one area but then transported to another area and deposited. Thus a full understanding of reef growth and structure requires a knowledge of not only accretion and erosion, but also of the dynamics of transport and deposition processes.

2.2.1 Reef accretion

Reef accretion involves the precipitation and deposition of organic and inorganic material which makes up the reef structure. Organic production has been extensively reviewed by Larkum (1983) and Hatcher (1988, 1990). Inorganic production, that of calcium carbonate ($CaCO_3$) is known as *calcification* and can occur through a variety of processes. The most obvious is the deposition of material by corals with the aid of their endolithic algae or zooxanthellae. However coralline algae also have a significant input, as does the process of lithification (Marshall, 1983). Calcification of the coral reef community as a whole has been reviewed by Smith (1983) while for input by corals see Chalker (1983) and coralline algae see Borowitzka (1983).

Over the past several decades the processes which govern reef accretion have been the focus of numerous studies (see Table 5a in Davies, 1983). As a result a range of techniques have been developed to provide estimates of reef growth, particularly in terms of carbonate deposition. Both Davies (1983) and Smith (1983) outline various methodologies which have been developed to estimate aspects of reef growth. Studies of reef calcification have provided estimates ranging from 0.8 kg m^{-2} yr^{-1} to 4 kg m^{-2} yr^{-1} (and even 10 kg m^{-2} yr^{-1}) (see Table 1 in Smith, 1983). Smith (1983) suggests that these values represent three different states of growth as not all areas of a coral reef are calcifying at the same rate and the same time. It is further proposed that at least 90-95% of the reef area is accreting at 0.8 kg m^{-2} yr^{-1} (slow), while only 4-8% is at 4 kg m^{-2} yr^{-1} (intermediate) and 1-2% at 10 kg m^{-2} yr^{-1} (fast). These rates of mass accretion can be converted into estimates of vertical accumulation and thereby comparable to linear growth estimates and radiocarbon dated core samples (Smith (1983).

2.2.2 Reef erosion

Although the different aspects of erosion which influence the reef structure are closely linked, they can be broadly categorised into three types (Trudgill, 1983). They are physical, chemical and biological. The first type considers physical abrasion of the reef substrate either by wave action (fracturing and moving carbonate material) or by the contact of loose fragments or *clasts* upon stable substrate and each other. A third possible physical process is that of salt weathering whereby the growth of salt crystals weakens the substrate (i.e., during evaporation (Trudgill, 1983)). Chemical erosion is the dissolution of the carbonate substrate by rain water and sea water. The final form of erosion is directly caused by the biota of the reef community. The biological destruction of reefs, termed as *bioerosion*, has recently been reviewed in detail by Hutchings (1986) and occurs either as chemical dissolution or mechanical abrasion of the substrate. In terms of impact it is now generally acknowledged that

bioerosion is the most important of the three processes when considering long term structural changes, but periodical physical erosion by storms is also an important, though infrequent, factor (Trudgill, 1983).

2.2.3 Sources of bioerosion

For an in depth discussion and review of bioerosion and its chief agents see Hutchings (1986). Eroding biota can be categorised into three groups according to their mode of action: grazers, etchers and borers. Principal grazing agents are herbivore and corallivore fish and echinoids. However, the bioerosion caused by their feeding habits may be deliberate or incidental. For example, corallivores such as, chaetodontids (butterflyfish) and tetraodontids (pufferfish and triggerfish) feed directly on growing coral polyps thereby directly ingesting substrate material (Randall, 1974). Algal grazers such as scarids (parrotfish) and acanthurids (surgeonfish) and echinoids feed on the abundant algae that cover patches of dead coral substrate. However, in addition to removing the algae, the scraping action of the fishes' teeth or the rasping action of the echinoids' Aristotle's Lantern also removes a proportion of the substrate (Ogden and Lobel (1978).

Several studies have attempted to quantify the rates of bioerosion by grazers. Tabulated lists of estimates of these studies can be seen in Davies (1983) and Trudgill (1983). Overall the estimated rates of erosion by grazing fish, such as parrotfish range from 40 g m^{-2} yr^{-1} (Frydl and Stearn, 1978) to 490 g m^{-2} yr^{-1} (Ogden, 1977). As these results would suggest, bioerosion by parrotfish can be variable for a given area of a reef which is complicated by fish density and habitat effects (Russ, 1984a,b). Erosion rates by grazing echinoids has been estimated from 24 g yr^{-1} (*Echinometra lacuncter* McLean, 1967), 0.11-0.9 g $urchin^{-1}$ d^{-1} (*Echinometra mathaei* Russo, 1980; Downing and El-Zahr,1987; Bak, 1990; McClanahan and Kurtis, 1991) and 8-14.5 g m^{-2} d^{-1} (*D. antillarum* Ogden, 1977; Stearn and Scoffin, 1977; Scoffin *et al.*, 1980). Other invertebrate grazers include gastropods, including limpets and chitons, but have a negligible influence compared to grazing effects by the larger fishes and urchins. Yet they may have important small-scale, local influences (i.e., affecting settlement success).

Bioeroders known as etchers include various bacteria, fungi and algae. The latter primarily being the endolithic algae found embedded in the tissues of growing corals. While these organisms can penetrate the reef substrate their actual direct impact upon the reef structure in terms of bioerosion is unclear and requires further study.

Various types of organisms found inhabiting the reef can be classed as borers. The principal members are sponges, bivalve molluscs, sipunculans and polychaetes (Hutchings, 1986). Research has shown that sponges appear to be the most important eroder of this type (Wilkinson, 1983). Highsmith *et al.* (1983) estimated that boring sponges were responsible for 85-94% of the skeletal excavation of three massive corals on the Belize barrier reef. Other borers, such as polychaetes, bivalves and sipunculans

accounted for the remainder. Actual estimates of $CaCO_3$ removal and conversion to sediment range from 13.4 kg m^{-2} yr^{-1} (Davies (1983) from data by Hudson (1977)) to 22-23 kg m^{-2} yr^{-1} (Neumann, 1966).

While these results give an indication of the magnitude of erosive impact the various organisms have upon the reef structure, the estimates should be treated with caution. Bioerosion does not occur at a continuous rate but is subject to various spatial and temporal effects (Hutchings, 1986). One obvious compounding factor is the distribution of the bioeroding organisms across the reef. For example, Russ (1984a,b) has shown the variability in distribution of grazing fishes across the central Great Barrier Reef. Furthermore, Kiene (1985) discovered that heaviest grazing by parrotfish occurred on the lagoonal patch reefs at Lizard Island, Great Barrier Reef. However, as pointed out by Choat (1983), feeding rate does not always correlate with fish density and therefore areas with high abundances of herbivorous fish does not necessarily mean a high bioerosion rate. However in the case of grazing echinoids, areas of high density will have a corresponding rate of bioerosion (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991). Furthermore studies of echinoids' feeding morphology and behaviour have shown that under food-limiting conditions (i.e., high population density) grazing effectiveness, and consequently bioerosion, is increased (Black *et al.*, 1982,1984; Levitan, 1991a). Other environmental conditions may also influence the feeding behaviour and therefore bioerosion rate of grazing organisms. For example, Hatcher (1981) revealed how fish grazing rates were seasonal and correlated with temperature (i.e. three-fold decline during the winter).

While the distribution of eroding organisms can alter due to migration, initial distribution, particularly those of more or less sedentary organisms, is largely influenced by recruitment success. The majority of the reef biota has a pelagic stage during their life-cycle, and the success rate and locality of settlement and recruitment of larvae is highly variable (Doherty, 1991). An important factor affecting the settlement of larvae, particularly for bioeroding organisms such as borers, is the availability of suitable substrate. This can vary temporally, as well as spatially across the reef, as substrate may only become available during certain times of the year (i.e., when no longer covered by winter algal growth; Coles, 1988). Hence the rate at which bioerosion occurs can also depend upon the time of year.

There are further compounding factors when the interactions amongst the bioeroding community are considered. Studies have revealed that there exists a distinct order of colonisation and succession by reef biota when an area of suitable substrate becomes available. For example, Risk and MacGeachy (1978) proposed the following sequence of succession for reefs in the Caribbean: bacteria - algae and fungi - clionid sponges and fungi - clionid sponges and spionid polychaetes - other sponges and eunicid polychaetes - mytilid bivalves, barnacles and sipunculans. Studies have also given an insight to the period of time involved in such successional processes. Hutchings and Bamber (1985) found that colonisation by sponges did not occur until the substrate had undergone boring by polychaetes for 9-12 months. Furthermore, Kiene and Hutchings (1994) revealed that high levels of grazing by other

bioeroders can maintain the boring community at an early successional stage, preventing the development of a climax community. This highlights the possible roles various groups of eroders have in modifying the substrate and thereby making it favourable for further colonization. Hence bioeroding communities are not stable over time, and researchers will need to consider this dynamical element in future studies.

2.2.4 Role of bioerosion

Bioerosion is a principal component of the various erosive processes that occur on coral reefs. However it is neither a discrete process nor a uniform one (Hutchings, 1986). Erosion by the reef biota is intrinsically linked with the other destructive processes. For example, erosion by grazers and borers weakens the reef substrate making it more susceptible to damage by physical and chemical processes. The converse is also true as physical and chemical erosion may facilitate eroding biota (i.e., by providing accessible substrate for settlement). Hence the combination of these processes produces a powerful erosive force which is continuously destroying the reef framework. If, therefore, the total rate of erosion exceeds the rate of reef accretion then net degradation of the reef will occur. For example Bak (1990) estimated the reef growth of a Moorean lagoon to be 6 g m^{-2} d^{-1}, while the bioerosion caused by the dominant echinoid population was calculated to be 12.5 g m^{-2} d^{-1} . Other studies have also demonstrated the risk of overall reef degradation when large populations of grazing echinoids are present (McClanahan, 1988; McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990).

Although initially destructive, the products of these forces are an important input to the processes of reef accretion. For example the detritus and sediment produced by bioerosion is an important source of material for lithification and cementation (Marshall, 1983). Indeed, Marshall and Davies (1982) discovered that for the One Tree Reef on the southern Great Barrier Reef sediment production for cementation was more important than material deposited by growing corals. Therefore while there is some export of eroded reef material the reef framework is continuously being eroded and recreated in a different form. This unceasing turnover of the reef helps to maintains its complex heterogeneous structure which in turn supports a rich species diversity (Connell, 1978). As highlighted earlier, bioerosion is not a uniform process, but exhibits spatial and temporal patterns involving localised disturbances. Thus across the reef system there will be areas of high and low rates of erosion. Superimpose these with the rates of reef accretion and it will be possible to see those areas where overall reef growth is occurring, as well as overall reef degradation and no net growth (i.e., a spatial insight to the continuously changing morphology of the reef). Combined with transport processes, bioerosion facilitates the spread of productivity across the reef (i.e., from high productive areas to low ones.

However while reef erosion can provide substrate for colonisation by eroding organisms it can also directly facilitate settlement by corals and other reef-building biota (Brock, 1979; Birkeland and

Randall, 1981; Sammarco, 1980; 1982b), and indirectly by the removal of competing sessile organisms, such as benthic algae (see section 2.1.3). In conclusion, therefore, erosive forces, particularly through bioerosion acting upon the reef system, are crucial in maintaining the heterogeneous nature of reef morphology. This in turn facilitates maintenance of high species diversity which characterises many coral reefs.

2.3 Biophysical features of the Arabian Gulf

The Arabian Gulf, also known as the Persian Gulf, or Iranian Gulf, or simply the Gulf, is a semi-enclosed body of water located between the landmasses of the Arabian peninsula and Asia. The area itself is known as the Arabian Region which encompasses five linked marine systems; the Arabian Gulf, the Gulf of Oman, the Arabian Sea, the Gulf of Aden and the Red Sea. The marine ecology of the Arabian Gulf has been reviewed in considerable detail by Sheppard *et al.*, (1992). Compared to the rest of the Indo-Pacific region, the Gulf is characterised by a low species diversity, the result of a combination of factors. Firstly, its semi-enclosed nature and peripheral location within the Indo-Pacific mean that colonisation from the rest of the Indian Ocean is restricted and much endemism has occurred. Secondly, the development of the Gulf's marine communities has been further delayed by their geologically recent reconnection to the ocean. Thirdly, and by far the most inhibiting factor, is the unusual climatic regime that holds sway over the region, resulting in the Gulf being the most arid region of the Indo-Pacific and experiencing some of the most extreme air and water temperature fluctuations known for coral reef ecosystems (Coles and Fadlallah, 1991). This section briefly highlights the key facts that are known for the Arabian Gulf and its reefs.

2.3.1 Geography

The coastlines of the Gulf are shared between seven countries; Iraq, Kuwait, Saudi Arabia, United Arab Emirates, Oman, Qatar, Iran and Bahrain. The Gulf is a relatively shallow sedimentary basin approximately 338 km wide and 1000 km long, usually divided into eastern and western sections by the Qatar peninsula. Despite a depth of about 100 m at the Straits of Hormuz and about 60 m in the northern trough along Iranian coast, the Gulf only has an average depth of approximately 35 m. As a result, most of the benthic habitats are in the photic zone. Indeed, it has been suggested that the Gulf is probably among the most productive of tropical marine systems (Sheppard and Price, 1991).

Underlying offshore saltdomes have pushed up numerous islands and substrates (Sheppard *et al.*, 1992). The most important are; an archipelago of barrier islands and tidal detritus north of the United Arab Emirates, the Hawar archipelago in the Gulf of Salwah south of Bahrain and the Saudi Arabian and Kuwaiti coral cays. These latter are islands with fringing reefs which rise from the sea floor to about 10-25 m deep. These coral cays provide the most diverse hard substrate habitats known in the Gulf (Sheppard *et al.*, 1992).

2.3.2 Geological history

In geological terms, the formation of the Arabian Gulf occurred fairly recently (Purser, 1973). However from 30 Ka the earth's sea levels fell to about 120-150 m below current levels, reaching its lowest at around 17 Ka. This lasted for around 7 Ka and consequently the entire Arabian basin was dried out around 18 Ka except for the northern end which received freshwater from the Tigris, Euphrates and Karuun rivers through the Shatt al Arab waterway. By about 15 Ka global surface temperatures increased again heralding the Holocene era. The associated rise in sea level occurred around 14-15 Ka which reached the present levels at around 7 Ka. Hence the current Gulf marine habitats and communities have only been in existence since 14-15 Ka when the area was re-colonised with the rising sea level.

2.3.3 Climate: atmospheric and hydrographic

The Arabian Gulf region lies at the edge of two or more global weather systems, and as a consequence is subject to major seasonal changes in the force and direction of both wind and water circulations (Sheppard *et al.*, 1992).

The main circulatory current in the Gulf is anti-clockwise in rotation and is driven by density gradients as well as surface (i.e. wind driven) effects (Reynolds, 1993). As proposed by Hunter (1986), water enters the Gulf, via the Straits of Hormuz, and travels up the Iranian coast until it reaches the northwest corner where it is diluted by the fresh water inputs of the Shatt al Arab. From there the water flows down the Kuwaiti and Saudi Arabian coastline until it reaches the shallow, southern embayments where high rates of evaporation increase the salinity and therefore density of the water. The heavier flows then sink to the bottom along the UAE coastline, finally exiting the Gulf beneath the incoming water. The tidal regime throughout the Gulf is generally diurnal to semi-diurnal which facilitates the reduction of environmental stress to shallow and intertidal inhabitants (i.e. tidal coverage during daylight hours in the summer when it is hottest, and vice versa in the winter when it is coldest) (Sheppard *et al.*, 1992).

The seasonal effects of local wind systems are more important to marine communities than the more regional weather patterns (Sheppard, 1993). For example, during the summer, strong afternoon winds develop which bring rough wave conditions to exposed shores. The winter is characterised by the *Shamal* winds, cold northerly flows which cause severe chilling and are responsible for the seasonal mortality of reef inhabitants (i.e. corals, Fadlallah *et al.*, 1995) but also trigger the profusion of various benthic algal species (Coles, 1988).

The above geological and hydrographical conditions impose an extreme environmental regime, the severity of which is markedly seasonal. Annual water temperature fluctuations in the Gulf are the

widest recorded for a region containing coral reef communities (Coles and Fadlallah, 1991; Fadlallah *et al.*, 1995). For example during the winter, at the inshore reefs in particular, the corals are regularly surviving temperatures at least 5 ^{0}C lower than the traditional limits of 18 ^{0}C (Coles, 1988). The salinity levels in the region also persist at levels known to inhibit coral growth (Kinsman, 1964) and limit coral distribution (Sheppard *et al.*, 1992; Price *et al.*, 1993). For example while the average salinity is approximately 38-45 ppt (John *et al.*, 1990), the southern embayment areas, where high evaporation occurs have been recorded at 55-70 ppt (Basson *et al.*, 1977; Jones *et al.*, 1978). Furthermore the sedimentary nature of the Gulf results in high levels of turbidity (Clarke and Keij, 1973; Basson *et al.*, 1977), particularly at the inshore reefs, which will further inhibit coral survival (Rogers, 1990).

2.3.4 Reefs of the Gulf

The occurrence of reefs in the Gulf has been reviewed by Sheppard and Sheppard (1991) and Sheppard *et al.* (1992), but for many areas records are not available. For example, in the eastern Gulf, Asian reefs have been reported from Qeshim Island in the Straits of Hormuz and Shotur Island, but there are likely to be many more, particularly along the Iranian coastline. Indeed it has been speculated that the Gulf's most developed fringing reefs are to be found along the steep Iranian coast (Sheppard *et al.*, 1992). The majority of the southern Gulf region is unsuitable for coral growth due to shallow water depth and predominance of soft sediments. However, numerous *Acropora* dominated patch reefs still occur, as well as fringing reefs around low lying islands and along the east and north coast of Qatar. Despite high coral cover, diversity is low (< 20 species) due to high sedimentation and mortality from winter air temperatures (Shinn, 1976). The reefs to the west of Qatar and around Bahrain have been described by Sheppard (1985) and Vousden (1988). There are numerous reefs on the north and northeast of Bahrain, though again, despite high coral cover, diversity is low (< 30 species). Only those offshore resemble typical reefs in their topography. In the Gulf of Salwah, the conditions are too saline for coral growth and the reefs are dominated by benthic algae.

The inshore and offshore reefs of the western Gulf are probably the most well-documented, particularly on the Saudi Arabian islands (Basson *et al.*, 1977; Burchard, 1979). These are true coral cays that, to date, contain the highest concentration of coral species known in the Gulf (approx. 50 species; Sheppard and Sheppard, 1991). Inshore patch reefs (i.e. Manifa) are considerably less diverse and more akin to those found around Bahrain (McCain *et al.*, 1984). The Kuwaiti islands have been described by Downing (1985), and in addition to having a low diversity (approximately 26 species, none of which are found below 15m), they are also the northernmost islands to be found in the Gulf.

2.3.5 Reef fauna and flora of the Gulf

(a) Fish

Compared to the rest of the Indo-Pacific, which has been estimated to contain in the region of 3000 species (Lieske and Myers, 1996), reef fish assemblages of the Arabian Gulf show a stark paucity. Smith *et al.* (1987) recorded only 72 species off the coast of Bahrain and Downing (1985) found 85 species on Kuwaiti reefs, while McCain *et al.* (1984) and Coles and Tarr (1990) found 106 and 101 species respectively off the east coast of Saudi Arabia. A more recent study on the Saudi Arabian reefs by Krupp and Almarri (1996) has increased the number to 281 species. Clearly, difference in size between the Gulf and the rest of the Indo-Pacific is a factor (in addition to the ecological ones), influencing species richness.

There are also distinct differences in the composition of the fish assemblages inhabiting marine habitats across the Gulf. For example, Coles and Tarr (1990) found that along the western Gulf coast the distribution of up to 50% of species was limited to either inshore or offshore reefs. The latter support nearly twice the abundance of individuals and diversity of species. Such trends and distributions have been correlated with reef development, habitat complexity and environmental stress (Roberts *et al.*, 1988; Coles and Tarr, 1990). Thus areas of high reef development and low environmental stress support the most diverse reef fish assemblages. But as Sheppard *et al.* (1992) point out, a large proportion of species in the Gulf such as *Diplodus sargus k.* (Sparidae) and *Scarus ghobban* (Scaridae), are not totally dependent on the reef for survival. In addition, the reef fish assemblages contain representatives from all the major herbivorous groups (i.e. Pomacentridae, Scaridae, Acanthuridae and Siganidae).

(b) Echinoderms

The systematics, biogeography and aspects of the ecology of echinoderms inhabiting the Gulf have been extensively covered by Price (1981, 1982a,b, 1983; Price and Rezai, 1996). Despite records of about 100 species for the region, only two are important herbivores of the reef community. Firstly, *E. mathaei*, a small, rock-boring urchin ubiquitous to the Indo-Pacific (Khamala, 1971) and, secondly, *Diadema setosum*, a large, long-spined urchin and a close relative of the extensively studied *D. antillarum* (Sammarco, 1982a,b; McClanahan and Muthiga, 1988; Levitan 1991a).

(c) Benthic marine algae

A revised checklist of the 207 taxa of marine algae found in the Arabian Gulf has recently been compiled by Basson (1992). However, due to the scarcity of algal literature that exists for the region, this list is only based on 16 papers that have been published over the last 149 years. To date most

research on benthic algae of the Arabian Gulf has been taxonomic (Basson, 1979a,b; Basson *et al.*, 1989; De Clerck and Coppejans, 1994; 1996), and few studies have investigated quantitative aspects of distribution, abundance, dynamics and regulation (but see Basson *et al.*, 1977). For example, various phaeophytes (i.e. *Sargasssum*, *Hormophysa*, *Cystoseiria*, *Colpomenia* and *Hincksia*) show markedly seasonal levels of growth and coverage, with maximums reached during the winter and spring (Sheppard *et al.*, 1992). Coles (1988) investigated the competitive effects of such seasonal algal growth on coral development, but was unable to elucidate the factors controlling the macroalgal blooms (although low temperatures were probably a critical element), and the extent to which competition for settlement space and light affects coral growth during such periods.

2.3.6 Reef communities and environmental stress

In the western Gulf, increasing gradients of environmental stresses such as salinity, temperature and sedimentation, have been associated with both a latitudinal (i.e. north to south) and a longitudinal (i.e. offshore to inshore) distance (McCain *et al.*, 1984; Downing, 1985; Sheppard, 1988; Coles and Fadlallah, 1991; Sheppard and Sheppard, 1991; Fadlallah *et al.*, 1995). Studies examining the composition of reef communities along these gradients have not only extended our knowledge of conditions particular species can tolerate and survive, but have also revealed the sequential changes in community composition and structure imposed by these environmental gradients.

For example, Sheppard (1988) determined the tolerance gradient of coral species to salinity in the Gulf of Salwah and Bahrain region. Only three species (*Siderastrea savignyana*, *Porites nodifera* and *Cyphastrea microphthalma*) were able to survive salinities up to 50 ppt. Similar salinity tolerance levels were also recorded by Kinsman (1964) along the coastline of the United Arab Emirates. Studies have also examined the effects of temperature on coral communities. Sheppard *et al.* (1992) has compiled data from various sources to produce an estimate of coral species survivorship under different ranges of temperature fluctuations. But as Coles and Fadlallah (1991) point out, not only are the extremes of the conditions experienced important, but also the duration of exposure. More recently, Fadlallah *et al.* (1995) have highlighted the compounding effects of aerial exposure during low tides when coincident with lowered temperatures, and suggest that in the Gulf such episodes may be the primary cause of observed coral mortality at shallow depths.

These environmentally imposed limits to coral distribution and growth have important implications for reef accretion and integrity. Sheppard *et al.* (1992) described how, as environmental conditions become more severe, the processes of coral growth and reef growth become uncoupled. Traditionally thought of as an accumulation of corals growing over the skeletons of their predecessors, reef growth is now considered as the binding and consolidation of sediment by corals, benthic invertebrates and algae (see section 2.2 above). However minimum conditions for reef growth are breached long before those which corals are unable to tolerate, and consequently communities still occur on reefs which are not

accreting. For example, reefs described by Sheppard (1985) in the Gulf of Salwah/Bahrain region, are composed of scattered coral colonies growing on pre-Holocene limestone reefs that are dominated by green and brown algae. This also leads to a contradiction of terms, as species traditionally classed as hermatypic or reef-building (i.e. *Acropora*), can occur in large abundance on reefs that are not accreting.

The transition of reef composition and structure that occurs in the western Gulf, from highly developed communities to their ultimate disappearance, along a southerly gradient to the Gulf of Salwah, has been described by Sheppard *et al.* (1992). The offshore reefs support the highest concentration of coral reef species, and are the best examples of continuing reef growth and development. However, with increasing proximity to the southern Gulf region and the Gulf of Salwah, definite changes occur in the coral community. The disappearance of *Acropora* species heralds increasing environmental stress, and the dominance by *Porites*, such as *P. nodifera*. However, coral cover does not necessarily decrease in this area, merely community diversity. With the advent of increasing salinity and turbidity, coral cover eventually declines until *Porites* is as equally abundant as the few other remaining genera, such as *Siderastrea* and *Cyphastrea*. Benthic algae 'capitalises' on this decline until conditions totally exclude corals and ultimately, brown algae are superseded by greens.

The extreme gradients of environmental stress that exist in the Gulf also have direct and indirect effects on other reef inhabitants. For example, the abundance of particular macroalgae (i.e. *Sargassum* and *Colpomenia*), is directly affected by pulses of changing abiotic conditions (i.e. lowering temperatures during winter), which trigger seasonal blooms. Indirectly, increasing gradients of environmental stress reduce the abundance of other inhabitants, such as corals and herbivores, which favours their increased abundance in such areas (see above). Of course in very extreme conditions, the environmental stresses will directly exclude even the most hardiest of benthic algae.

For other inhabitants, such as reef fish, increasing environmental stress can directly cause adult and larval mortality (i.e. due to low temperatures and high salinity; Sheppard *et al.*, 1992) and therefore affect distribution and recruitment. Indirectly, distribution can be affected by decreasing habitat quality (i.e. coral growth and reef development; Roberts *et al.*, 1988) in response to environmental gradients (Sheppard, 1988). Similarly for echinoderms, abiotic conditions can directly induce physiological responses, such as dwarfism (Price, 1982a), and indirectly affect distribution by limiting fish predators and therefore reducing predation pressure.

Assemblage	Functional Groups		Common Genera
TURF	AG 1	Microalgae (single cell)	Diatoms, Cyanobacteria
	AG 2	Filamentous algae (uniserate)	*Cladophora*, *Sphacelaria*, *Bryopsis*
MACROALGAE	AG 3	Foliose algae (single layer)	*Ulva*, *Enteromorpha*
	AG 3.5	Corticated foliose algae	*Dictyota*, *Padina*, *Lobophora*
	AG 4	Corticated macrophytes (terete)	*Chondria*, *Laurencia*, *Caulerpa*
	AG 5	Leathery macrophytes	*Sargassum*, *Turbinaria*
	AG 6	Articulated calcareous algae	*Corallina*, *Halimeda*, *Jania*
CRUSTOSE	AG 7	Crustose algae	*Lithothamnion*, *Peyssonnelia*, *Porolithon*

Table 2.1: **Functional groups** of benthic marine **algae** common on coral reefs (adapted from Steneck, 1988; Steneck and Dethier, 1994).

Main gut components	Acanthuridae	Scaridae	Siganidae	Pomacentridae	Blennidae
Algal turfs	52%	-	100%	96%	27%
Turfs, detritus and inorganic material	28%	94%	-	-	33%
Macroalgae	14%	-	-	4%	7%
Detritus	7%	-	-	-	33%
Seagrass	-	6%	-	-	-
No. of species	29	19	4	24	15

Table 2.2: Food preference (main gut component) by taxonomic groups of herbivorous fish, given as a percentage of the number of species examined for each group (adapted from Russ and St. John (1988).

(a)

Herbivore size	Example groups	Foraging range	Grazing frequency
Microherbivores	Amphipods, Limpets	Small	High
Intermediate herbivores	Pomacentrids, Urchins	Medium	Medium
Macroherbivores	Scarids, Acanthurids	Large	Low

(b)

Effectiveness	Example groups	Common genera
Non-denuding	Pomacentrids, Gastropods, Amphipods, Polychaetes	*Stegastes*, *Pomacentrus* *Nerita*, *Tectarius*
Denuding	Acanthurids, Siganids Pomacentrids, Blenniids	*Acanthurus*, *Siganus* *Microspathodon* *Ophioblennius*
Excavating	Scarids, Echinoids, Limpets, Chitons	*Scarus*, *Sparisoma* *Diadema*, *Echinometra* *Acmaea*, *Acanthochitona*

Table 2.3: Classification systems for herbivore functional groups based on (a) foraging ranges and grazing frequency (adapted from Carpenter, 1983; 1986), (b) grazing effectiveness (adapted from Steneck, 1983; 1988).

Chapter Three

Study Sites

3.1 Introduction

Despite the extreme conditions prevailing in the Gulf (Chapter 2.3), a variety of coral reef types are found. These range from algal dominated inshore patch reefs to the offshore coral cays that support the highest levels of species diversity (Sheppard *et al.*, 1992). This range is primarily due to the inverse relationship between coral reef development and environmental stresses such as salinity, turbidity and temperature (Sheppard, 1988). Elevated salinity, turbidity and extremes of temperature are the conditions which characterise the inshore areas, and hence these contain the most undeveloped and species-poor reefs. Study sites were therefore not only chosen to examine the effects of depth and distance from the shore (Chapter 1), but also to encompass the extremes of coral reefs found in the Gulf. Patch reefs were not included, largely for logistical reasons.

3.2 Inshore reef site

The inshore study site is located on the northern shore of Abu Ali Island (Figure 3.1; Plate 3.1), where a narrow fringing reef extends for over 8 km in length and approximately 10-50 m in width (27°21'05'' N 49°30'55'' E). The shallow reef is fragmented into strips and patches of various lengths and diameters and is subjected to high wave exposure, resulting in a high level of sedimentation. It is predominantly composed of eroded beach and coral rock with an average coral cover of 19% (Vogt, 1994a; 1996). While several coral species are represented, the reef is dominated by *Porites compressa* which is mainly found on the seaward edge. This reef system was chosen, not only as representative of the inshore reefs in the area, but also due to its previous use in other scientific studies (Krupp and Müller 1994; Krupp *et al.*, 1994; Vogt, 1994a,b; Krupp and Almarri, 1996; Vogt, 1996) and accessibility. A full description of inshore reefs of the Saudi Arabian Gulf, and in particular those of Abu Ali, can be found in Basson *et al.* (1977) and Vogt (1994a; 1996) respectively. The inshore reef site was approximately 50 m from the beach, 15 m in width and has a depth of 1.5 m (Plate 3.1). The shallow nature of the site meant that it was greatly influenced by tides, such that during extreme spring tides upper layers of the reef would become exposed (Plate 4.0).

3.3 Offshore reef sites

The two offshore study sites are located on the southern, leeward side of Jana Island (Figure 3.1; Plate 3.2), which lies approximately 12 nautical miles east of Abu Ali Island (27°21'50'' N 49°54'0'' E). The reefs of Jana and the other four cays harbour the most diverse coral communities found in the

Arabian Gulf. A full description of their zonation and habitats can be found in Basson *et al.* (1977) and Vogt (1994a,b; 1996). The first offshore study site was located at the shallow reef edge and upper buttress zone (Basson *et al.*, 1977) at a depth of approximately 2-3 m. This area is predominantly covered with colonies of *Acropora*, *Pocillopora*, *Porites* and *Platygyra*, with an average live coverage of approximately 35 % (Vogt, 1994a; 1996). The second study site was located at the base of the reef slope zone (Basson *et al.*, 1977) at a depth of approximately 11-13 m and is predominantly covered with colonies of *Montipora*, *Acropora*, *Pocillopora* and *Pavona*. As all the offshore coral cays show similar reef structure and composition, Jana Island was chosen for its closer proximity to the mainland, thereby facilitating access, and in view of its previous use in other recent scientific studies (Krupp and Müller 1994; Krupp *et al.*, 1994; Vogt, 1994a,b; Krupp and Almarri, 1996; Vogt, 1996). Furthermore, the sheltered leeward side of the island offered more suitable study sites for field observations and experimental work than the exposed windward side.

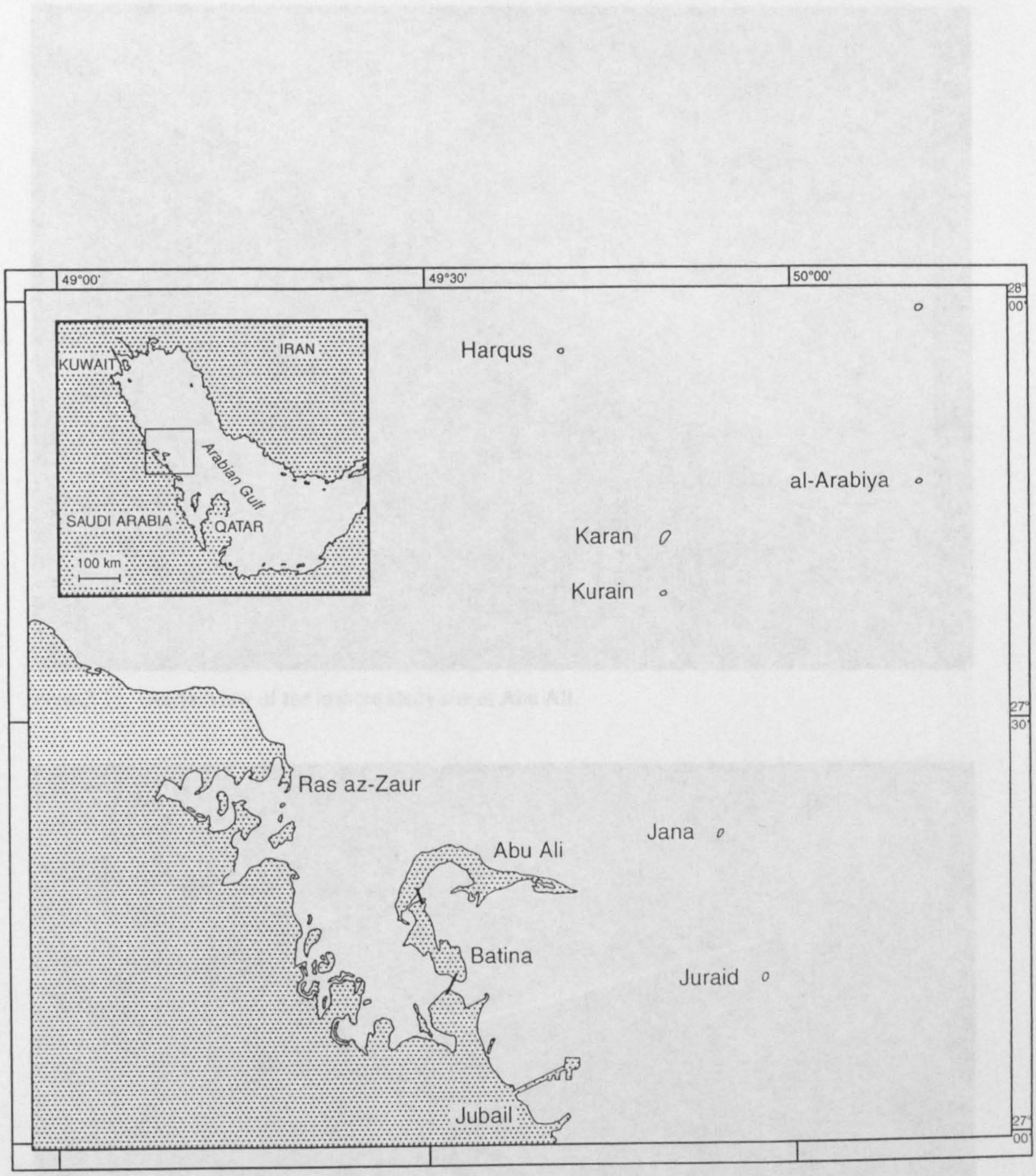


Figure 3.1: **Map of the Saudi Arabian Gulf coast** and study sites with insert of the Arabian Gulf (from Krupp *et al.*, 1996).

Plate 3.1: Aerial view of the inshore study site at Abu Ali.

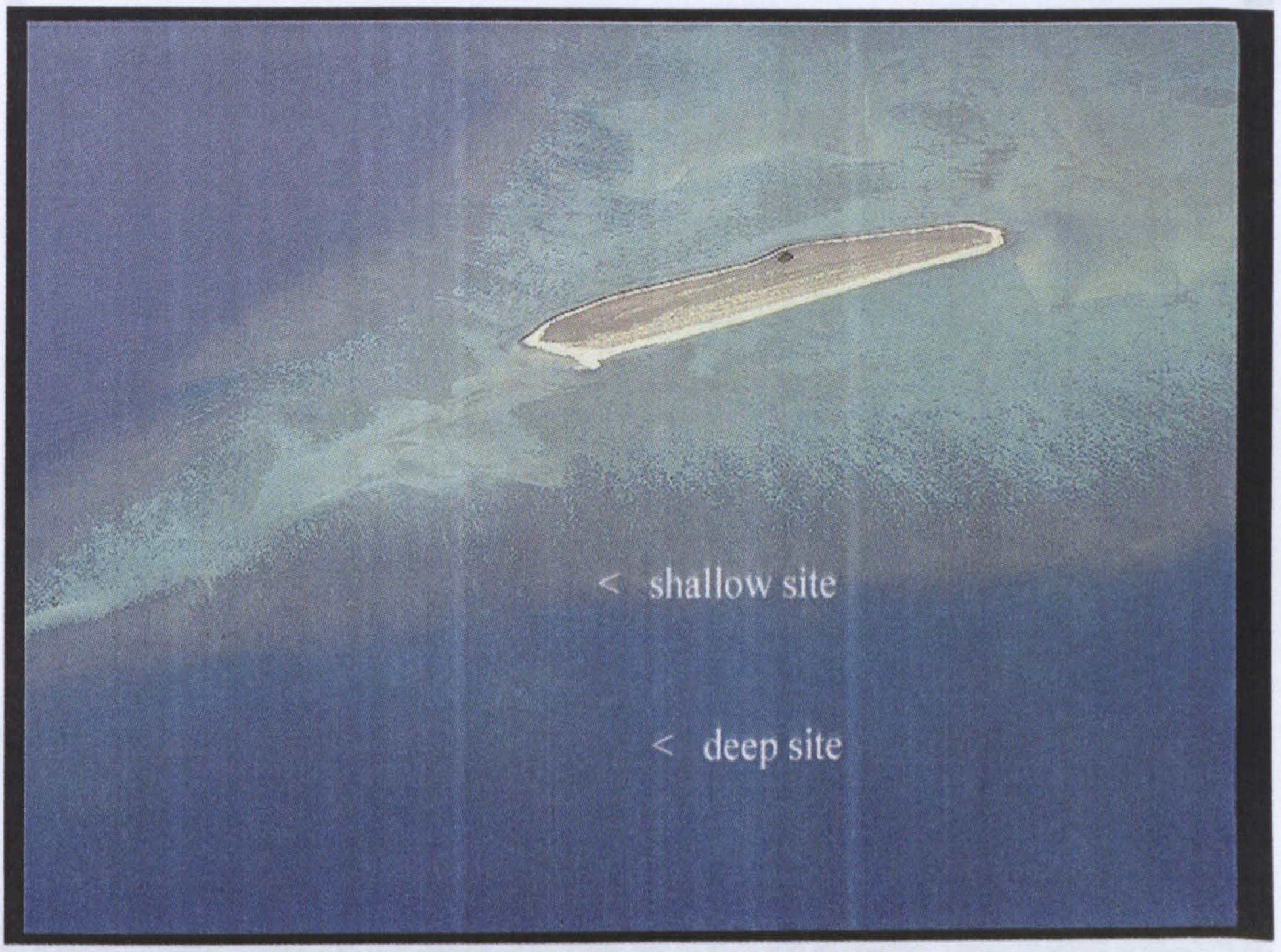


Plate 3.2: Aerial view of the offshore study sites at Jana.

SECTION TWO

Abiotic Conditions

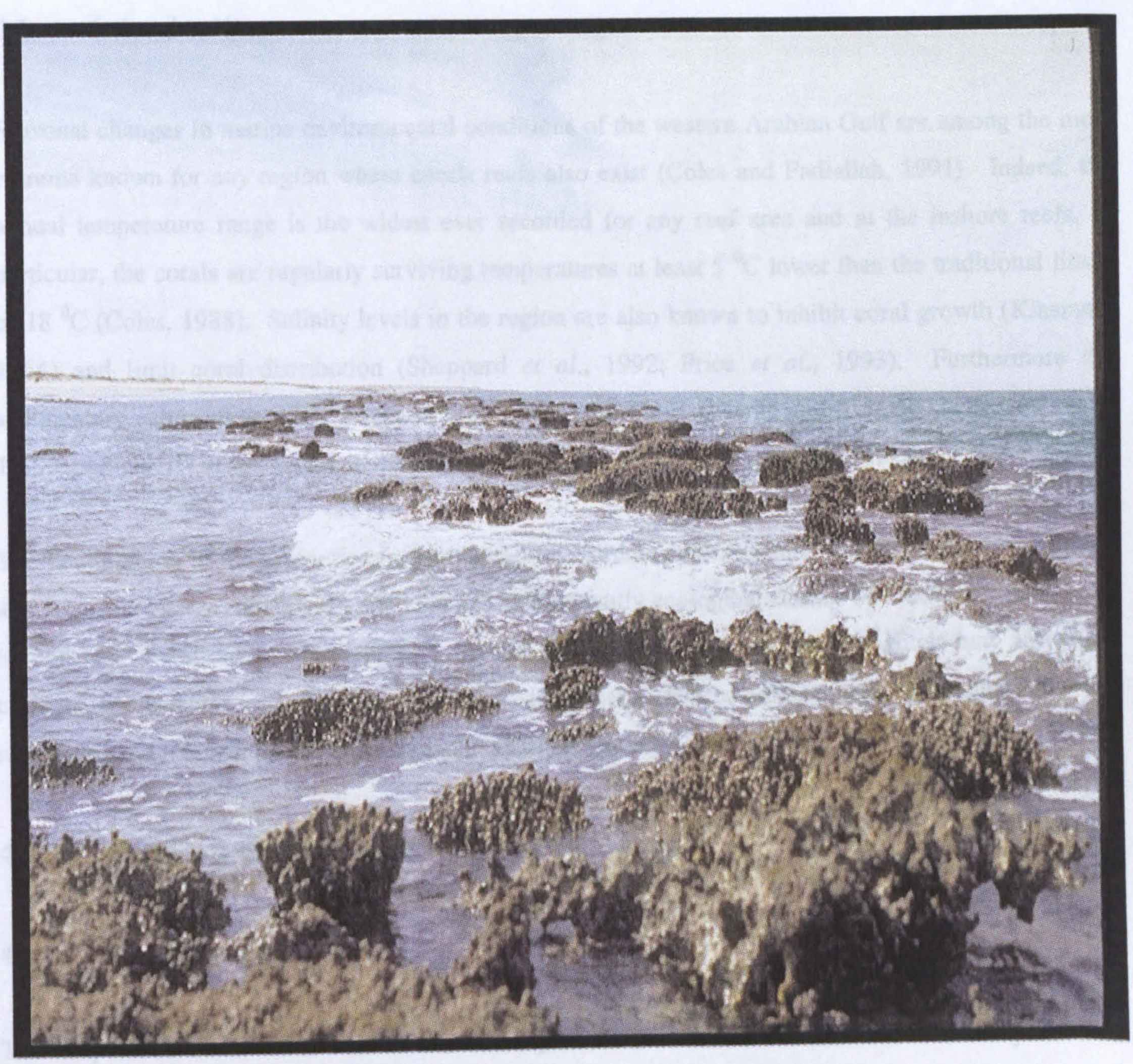


Plate 4.0: Inshore fringing reef at Abu Ali during an extreme low tide (13/12/94).

Chapter Four

Abiotic Conditions

Summary

Measurements of subtidal water temperature and salinity at the three study sites were conducted throughout the 12-month study period. At the inshore reef mean temperature and salinity was 25.41 ± 1.47 ^{0}C and 42.85 ± 0.20 ppt, while at the shallow and deep offshore reefs temperature and salinity means were 27.06 ± 3.59 ^{0}C and 40.79 ± 0.53 ppt, and 26.61 ± 3.44 ^{0}C and 40.62 ± 0.63 ppt respectively. Sedimentation rates at the three study sites were also determined during winter/spring. The inshore study site at Abu Ali experienced greatest fluctuations in all three abiotic conditions, which was attributed to its shallow nature and greater exposure to prevailing winds and currents.

4.1 Introduction

Seasonal changes in marine environmental conditions of the western Arabian Gulf are among the most extreme known for any region where corals reefs also exist (Coles and Fadlallah, 1991). Indeed, the annual temperature range is the widest ever recorded for any reef area and at the inshore reefs, in particular, the corals are regularly surviving temperatures at least 5 ^{0}C lower than the traditional limits of 18 ^{0}C (Coles, 1988). Salinity levels in the region are also known to inhibit coral growth (Kinsman, 1964) and limit coral distribution (Sheppard *et al.*, 1992; Price *et al.*, 1993). Furthermore the sedimentary nature of the Gulf results in high levels of turbidity (Clarke and Keij, 1973; Basson *et al.*, 1977), particularly at the inshore reefs, which will further inhibit coral survival (Rogers, 1990).

The combination of these abiotic conditions impose extreme environmental stress upon the coral reefs and their inhabitants (Sheppard *et al.*, 1992). Consequently ecological studies on Gulf coral reefs need to consider variations in these natural stresses in addition to other factors which may influence community structure and function. In this study, temperature, salinity and sedimentation were monitored and recorded at the three study sites throughout a 12-month period (May 1994 - May 1995).

4.2 Materials and Methods

4.2.1 Temperature

The temperature of the water column immediately above the substratum surface at each study site was measured (to 0.1 ^{0}C) using a mercury-based, hand-held, glass thermometer. Between May 1994 and May 1995 measurements at Abu Ali were taken twice a week, while at the two offshore sites at Jana Island measurements were taken twice a month.

4.2.2 Salinity

Samples of water were collected from the water column immediately above the substratum surface at each study site using an empty, pre-sealed plastic bottle. On return to the laboratory, the salinity of each sample was measured (to 0.5 ppt) using a Salinity Hand Refractometer (No. 1270G). Between May 1994 and May 1995, measurements at Abu Ali were taken twice a week, while at the two offshore sites at Jana island, measurements were taken twice a month.

4.2.3 Sedimentation

Sediment traps were constructed using plastic pipe approximately 40 cm long and 4 cm in diameter, the ends of which could be capped and sealed tight with plastic lids. These were then secured to the substratum at the three study sites. At the offshore sites, this was by attachment to the sides of one of the exclusion cages (described in Chapter 6) with the aid of plastic tie-wraps. At Abu Ali, the traps were secured to the concrete blocks (Plate 4.1), again with the aid of plastic tie-wraps. In February 1995 two traps were established at each study site and left for eight weeks (approx. 19 February - 13 April), after which the contents of each trap was washed and dried to a constant mass on pre-weighed hardened, ashless filter paper (Whatman No. 51) at 60 ^{0}C.

4.3 Results

4.3.1 Temperature

Over the 12-month recording period, temperature fluctuations were measured at all three study sites (Figure 4.1). However the greatest change was observed at Abu Ali, with a recorded maximum and minimum of 33.6 ^{0}C and 13.4 ^{0}C respectively. This contrasts with Jana, where extremes of 32.4 ^{0}C and 18.9 ^{0}C, and 32.2 ^{0}C and 18.7 ^{0}C were recorded at the shallow and deep sites respectively. The average temperatures over the 12-month study period for each site are given in Table 4.1.

4.3.2 Salinity

Seasonal changes in salinity at the three study sites over the 12-month period are shown in Figure 4.2. Greatest fluctuations were observed at Abu Ali, with a recorded maximum and minimum of 45 ppt and 41 ppt respectively. In contrast, at Jana maximum salinities of 42 ppt (shallow site) and 42 ppt (deep site), and minimum salinities of 40 ppt (shallow site) and 39 ppt (deep site) were recorded. The average salinities over the 12-month study period for each site are given in Table 4.1.

4.3.3 Sedimentation

The inshore site at Abu Ali had the highest sedimentation rates, with a two-fold and ten-fold difference between the shallow and deep offshore sites respectively (Table 4.1). Unfortunately these findings are only based on single readings, as one of the sediment trap replicates was damaged at each study site and had to be excluded from the results.

4.4 Discussion

The ranges for the abiotic conditions recorded during the 12-month study period (May 1994 - May 1995) are consistent with those previously reported from the region (Kinsman, 1964; Downing, 1985; Coles, 1988; John *et al.*, 1990; Coles and Fadlallah, 1991; Reynolds, 1993). For example, Coles (1988) found that inshore and offshore reefs along the Saudi Arabian coast experienced temperature and salinity ranges of 13.5-36 ^{0}C and 39-46 ppt, and 17-34 ^{0}C and 39.5-41 ppt respectively.

The wider fluctuations observed at Abu Ali are primarily due to the shallow depth of water over the fringing reef and also its northwestern orientation. During winter, in particular, the prevailing northern or *Shamal* winds cause severe chilling and mixing of any thermally stratified layers (Reynolds, 1993; Sheppard, 1993). In summer such mixing of the layers may be beneficial, but in the winter this allows the colder water to permeate the water column. It also increases turbidity which imposes further environmental stress (Rogers, 1990). However the irregular diel nature of the tides in the region can alleviate the worst of temperature induced stress. In summer, high tides cover the shallow areas in daytime and expose them at night, while it is the reverse in winter (Sheppard, 1993). Nevertheless, conditions are still severe. During this study, for example, the lowest recorded temperatures occurred during a diurnal low tide, when the water temperature dropped to 13.4 ^{0}C and the air temperature around the exposed coral heads was only 10.8 ^{0}C .

In contrast, the study sites on the offshore island are distant from the restricted, shallow, nearshore bays. Their location on the leeward side of the island, exposure to stronger currents and water circulation, and adjacent deeper water all combine to alleviate the adverse effects of temperature, salinity and turbidity. Consequently the severity of these conditions, while showing similar trends to those experienced at the inshore study site, are much reduced.

All three environmental parameters, temperature, salinity and turbidity, directly limit coral growth and diversity, and consequently reef structure and development. Sheppard (1988) illustrated the transition that occurs in coral communities of Arabian reefs in response to an increasing environmental gradient encompassing the above parameters; from a species-rich coral reef dominated by *Acropora*, to a species-poor reef dominated by algae. However it is not only corals and coral reefs that are affected by such environmental stresses, but also other marine ecosystems and their inhabitants. For example, at

the community level the species diversity of organisms living in seagrass and soft-bottom habitats is inversely correlated with salinity (Coles and McCain, 1990), while at the level of the individual, high salinity stress has also been found to induce dwarfism in echinoderms (Price, 1982b). The relative influence of temperature, salinity and sedimentation on reef biota at the three study sites is discussed further in Chapter 11.

Study site	**Mean temperature** (^{0}C)	**Mean salinity** (ppt)	**Sediment weight** (g day^{-1})
Abu Ali	25.41 ± 1.47 (6.46)	42.85 ± 0.20 (0.84)	0.69
Jana (shallow)	27.06 ± 3.59 (5.34)	40.79 ± 0.53 (0.84)	0.32
Jana (deep)	26.61 ± 3.44 (5.22)	40.62 ± 0.63 (1.04)	0.06

Table 4.1: Mean **temperature** and **salinity** (x ± 95 % confidence limits, SD in parentheses) and dry **sediment weight** recorded at each study site.

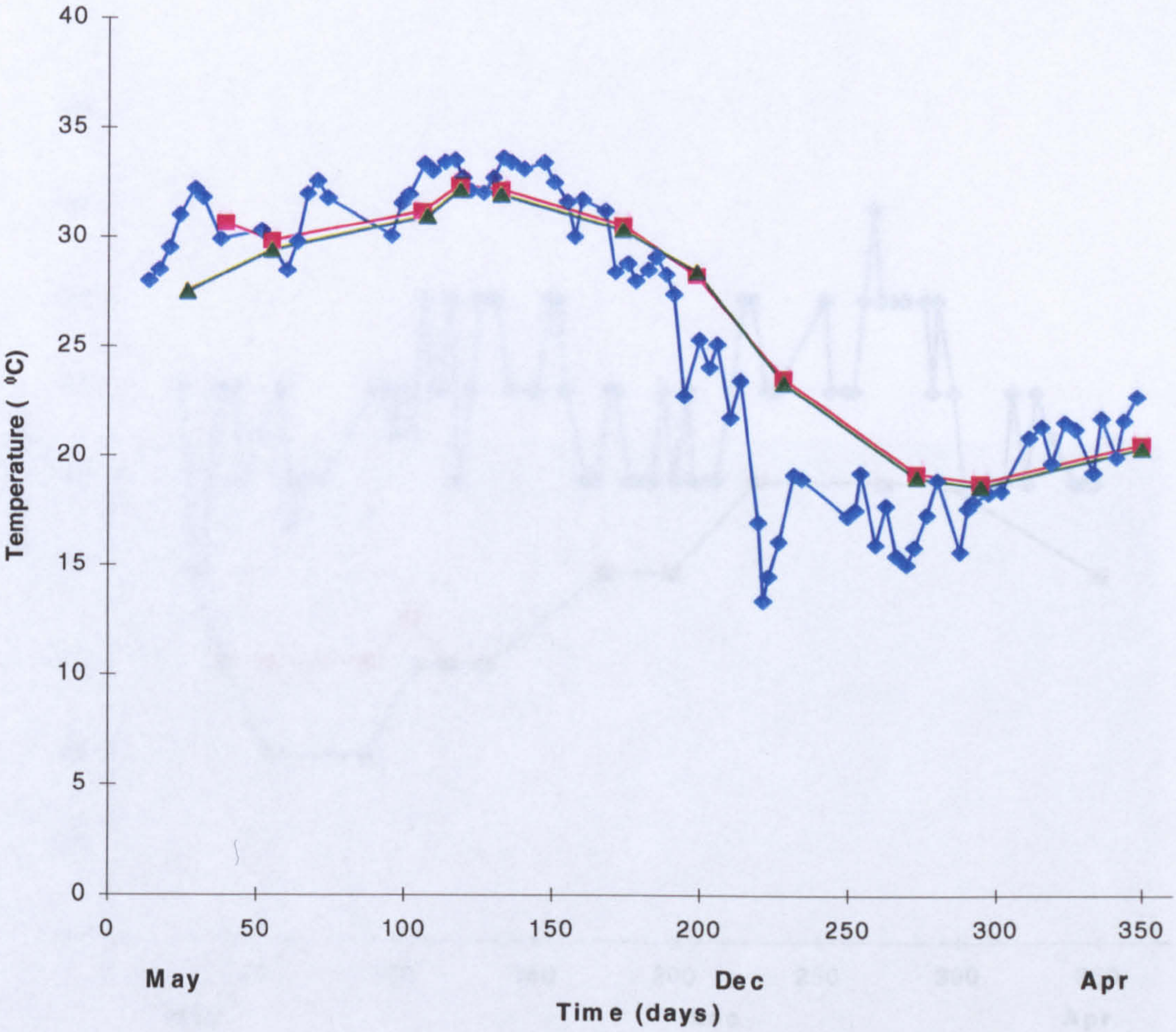


Figure 4.1: **Water temperature** immediately above the substratum at the three study sites during the study period; (◆) Abu Ali, (■) Jana (shallow), (▲) Jana (deep).

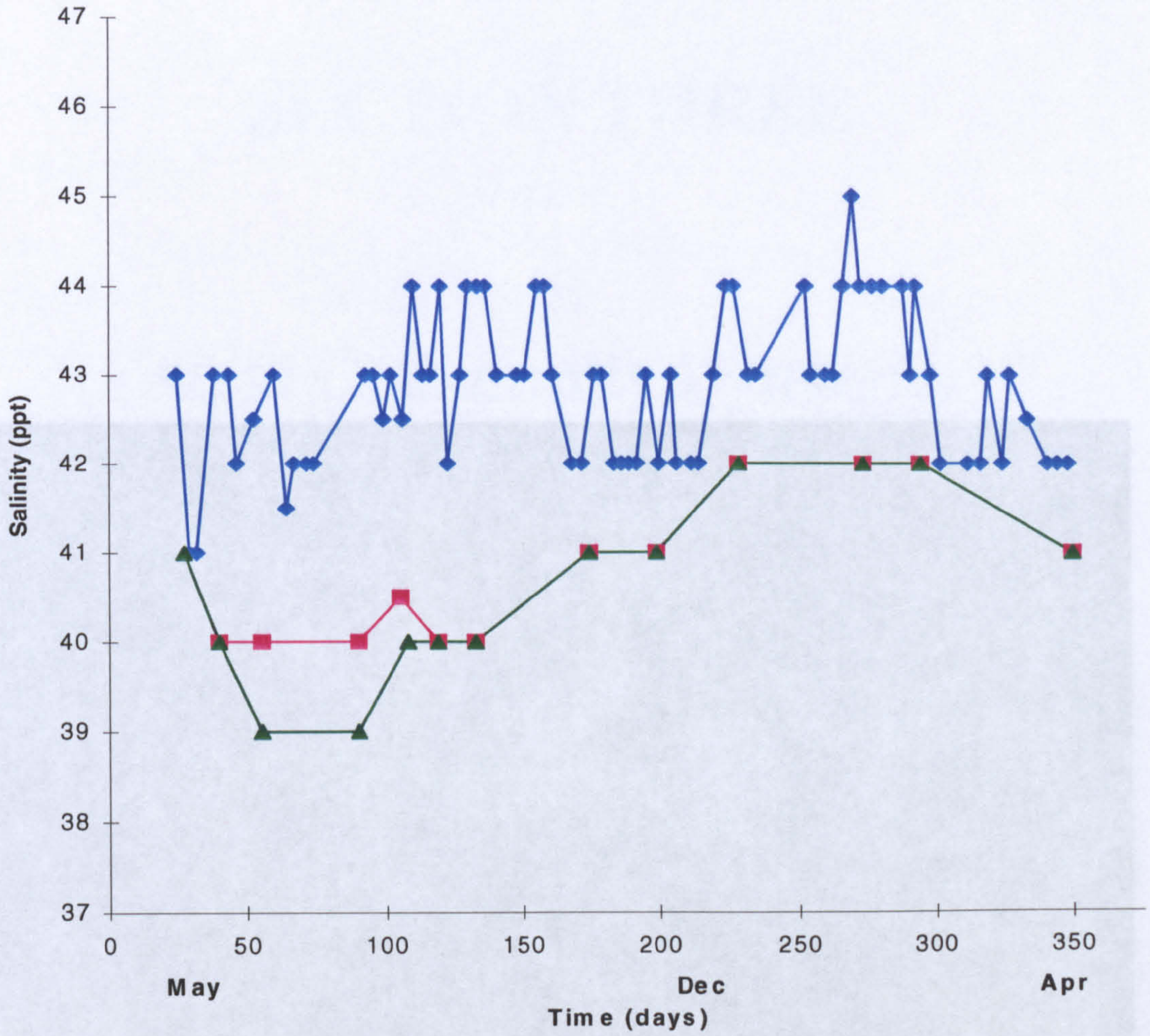


Figure 4.2: **Salinity** immediately above the substratum at the three study sites during the study period; (◆) Abu Ali, (■) Jana (shallow), (▲) Jana (deep).

Plate 4.1: Two sediment traps attached to concrete blocks at the inshore study site at Abu Ali (11/1/95).

SECTION THREE

Algal Community Dynamics

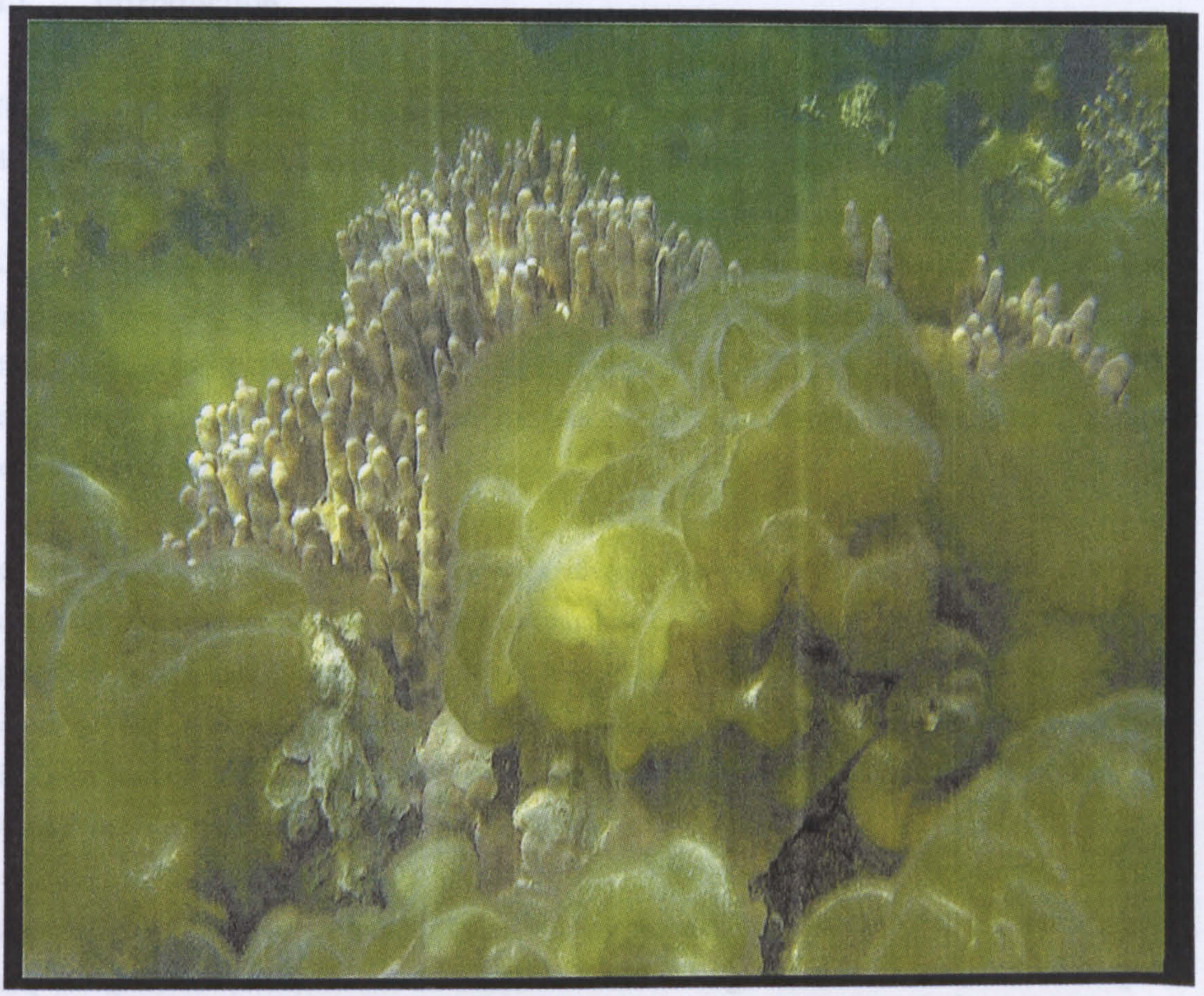


Plate 5.0: Seasonal growth of macroalgae, *Colpomenia sinuosa* and *Hincksia mitchellae*, obscuring *Porites* colonies on the inshore fringing reef at Abu Ali (2/2/95).

Chapter Five

Effects of seasonality and location

Summary

The generic composition and structure of the epilithic algal community was monitored on inshore and offshore reefs throughout a 12-month period using algal settlement plates. Communities at the two offshore sites showed greatest similarity, both being characterised by a low standing crop dominated by crustose forms. The inshore algal community, while dominated by filamentous genera, was more akin to the shallow than the deeper offshore community. Location (i.e. distance from the shore) appeared to be more important than seasonality in determining the structure and composition of the epilithic algal community.

5.1 Introduction

The communities of benthic marine algae commonly found on the substratum of coral reefs are characterised by a mixture of algal assemblages and functional groups (Table 1a, Steneck, 1988). These range from low biomass, crustose coralline dominated communities (Scott and Russ, 1987; Klumpp and McKinnon, 1992) to high biomass stands of macroalgae (Martin-Smith, 1992). However the most common algal assemblage encountered is the 'algal turf', a mixture of primarily filamentous algae (Borowitzka, 1981). The epilithic algal community (EAC) is the term given to the mixed standing crop of filamentous, fleshy, corticated and crustose algae, usually no greater than 10 mm in height (Steneck 1988).

Studies have shown that while algal species diversity is generally high throughout coral reef ecosystems, comparison between different communities at the generic level reveals that the EAC is comprised of common elements (Carpenter, 1981; Hay, 1981b; Sammarco, 1982a; Hatcher and Larkum, 1983; Lewis, 1986; Morrison, 1988). For example Scott and Russ (1987), while working on the Great Barrier Reef, found various genera from the Rhodophyta, Chlorophyta, Phaeophyta and Cyanophyta, in common with studies from the Caribbean.

A revised checklist of the 207 taxa of marine algae found in the Arabian Gulf has recently been compiled by Basson (1992). However, due to the scarcity of algal literature that exists for the region, this list is only based on 16 papers that have been published over the last 149 years. To date most research on the benthic algae of the Arabian Gulf has been taxonomic (Basson, 1979a,b; Basson *et al.*, 1989; De Clerck and Coppejans, 1994; 1996), and few studies have investigated quantitative aspects of distribution, abundance, dynamics and regulation (but see Basson *et al.*, 1977). For example, Coles (1988) investigated the competitive effects of seasonal algal growth on coral development.

In this study the generic composition and seasonal changes of the epilithic algal community were monitored at the inshore and two offshore study sites. Its aim was to assess community dynamics and determine whether any differences between the study sites were primarily the result of seasonal or geographic (i.e., inshore vs. offshore) effects.

5.2 Materials and methods

5.2.1 Experimental Design

In November 1993, six panels covered with 344 algal settlement plates were equally distributed between the three study sites (i.e. two replicate panels at each location). Except for the number of settlement plates placed at each site, the experimental design was identical. Each settlement plate was a plain, unglazed ceramic tile (7.5 cm x 7.5 cm), and all plates were labelled on the underside with a permanent marker pen and secured to the six square metal panels. Each panel consisted of galvanised wire mesh (1.3 cm mesh diameter) bound to a square aluminium frame with single-stranded galvanised wire. Each plate was secured to the wire mesh with plastic cable-ties (10 cm long and 2.5 mm wide); two such ties at opposing corners, clamping the ceramic plate to the wire beneath. This method of attachment incurred the minimum loss of surface area of the plate for algal settlement. At the offshore island of Jana, each wire panel was 61.5 cm^2 in size and covered with 36 plates (arranged in a 6 x 6 grid; Plate 5.1). Attachment to the substratum was achieved using metal stakes (30 cm long) hammered into the reef at the corner of each panel. The latter were then secured to the stakes with plastic cable-ties (18 cm long and 5 mm wide). At the inshore fringing reef along Abu Ali Island, each wire panel was 92 cm^2 in size and covered with 100 plates (arranged in a 10 x 10 grid). However the compact nature of the beach rock substratum at Abu Ali prevented use of metal stakes. Instead, each panel was weighted down with two cement blocks (40 cm x 20 cm x 20 cm in size) diametrically secured to the aluminium frame with plastic cable-ties (18 cm long and 5 mm wide; Plate 5.2).

The open design of the panels and their close proximity to the surface of the substratum was assumed to allow unhindered access to the settlement plates by the macroherbivores (Plate 5.3), and therefore exposing them to a normal level of grazing activity. All panels were left for five months in order to acquire a natural growth of algae. Monitoring of the algal community growing on the settlement plates began in May 1994 and continued for a total period of twelve months. During sampling a single plate was randomly selected from each replicate panel (i.e. a total of two per sample), the algal community growing upon it investigated (see section 5.2.2), and then replaced in order to keep the surface area available to grazers and colonising algae constant. At the inshore site, sampling was undertaken twice a week while at the offshore sites plates were removed once every two weeks.

In order to monitor any seasonal growth, colonisation and the relative abundance of larger macroalgae (i.e., phaeophytes), a 50 m transect at Abu Ali (see Chapter 8) was monitored at irregular intervals throughout the year. In each case, the percentage cover by different macroalgae within a 1 m^2 quadrat placed every 2 m along the transect, was recorded (Plate 8.1).

5.2.2 Sample analysis

Plates removed and taken to the laboratory were kept under aeration in fresh sea water while awaiting analysis. The abundance of algal genera growing on the individual plates was estimated using the point intercept method (see Dodge *et al.*, 1982; Carpenter, 1986). In this case, twenty-five random points were chosen from a 14 x 14 grid laid over the whole surface area of the plate, and all genera beneath each point were recorded. In addition, the height of each sampled alga was measured and recorded in terms of a size class (SC) category as follows: SC1 <1 mm; SC2 1-3 mm; SC3 3-6 mm; SC4 6-10 mm; SC5 >10 mm.

5.2.3 Data analysis

Algal abundance was expressed as the number of genera occurring on each plate and as a percent cover of the surface area for each genus and the entire plate. It is important to note that pooling of replicate plates resulted in an additive estimate of abundance, based on the total number of different genera occurring on the two replicates. Volumetric cover (i.e., size class x surface cover) was also estimated for each recorded genus.

The degree of similarity of the algal composition between communities was calculated using the Percent Similarity or Renkonen Index (Renkonen, 1938; Equation 1).

$$P = \Sigma \text{ minimum } (p_{1i}, p_{2i}) \qquad (1)$$

where; P = percentage similarity between samples 1 and 2

p_{1i} = percentage of species i in community sample 1

p_{2i} = percentage of species i in community sample 2

Despite its simplicity, this coefficient of similarity was used in preference to others (i.e., Bray-Curtis Measure), as it has been shown to relatively little affected by sample size and species diversity (Wolda, 1981; Krebs, 1989). The calculation involves the abundance of each species (i.e. presence/absence, percentage cover, biomass) being standardised as a percentage of the community sample, such that the total of these relative abundances equals 100 %. These values are then entered into Equation 1, where the percent similarity is equal to the summation of the minimum value in each pairwise combination of the species in each community sample. Statistical analysis of the data involved Model I Analysis of

Variance (ANOVA) for all parameters describing the algal community composition between location (i.e. study site) and over time. Correlation analysis was also used to investigate linear temporal relationships.

5.3 Results

5.3.1 Effects of substratum

Prior to the seasonal analysis of the algal community growing on the settlement plates, a comparison was made with the community growing on the surrounding natural substratum at the three study sites. At the beginning of the experiment, when the settlement plates had acquired five months growth of algae, there was no significant difference for either percent surface cover by each genus, or the total surface cover at any of the sites (Table 5.1). However, at the end of the experiment twelve months later, the natural substratum at the shallow offshore site had a significantly larger percent surface cover by each genus and total surface cover in comparison with the algal community growing on the settlement plates. At the other sites there were no significant differences at the end of the experiment.

There was also no significant difference at the beginning of the experiment for either the volumetric cover by each genus, or the total volumetric cover at any of the sites, except for the total algal cover at Abu Ali (Table 5.2). In this case the total cover on the settlement plates was (just) significantly greater than the natural substratum ($p = 0.0498$). At the end of the experiment there was again a significantly greater total volumetric cover, and cover by each genus, on the natural substratum compared with the settlement plates at the shallow offshore site.

The degree of similarity between the communities growing on natural and artificial substrata at the three study sites was further investigated using the percent similarity index. Both surface cover (Table 5.1) and volumetric cover (Table 5.2) revealed an increase in similarity between the beginning and the end of the experiment. In terms of surface cover, the Abu Ali and Jana (shallow) sites both showed the largest increase and the Jana (deep) site the least. However, in terms of volumetric cover Abu Ali showed the smallest increase while Jana (shallow) again showed the greatest. In general, the percent similarity estimates for volumetric cover were lower than those based on percent surface cover.

3.3.2 Effects of seasonality and location

The composition of the algal community on the settlement plates varied significantly over time as well as between study sites (Table 5.3). There was a significant difference in the number of genera, the percent surface cover and the volumetric cover between each location. The only significant temporal relationships were with the percent surface cover and volumetric cover, as the number of genera at the three sites did not vary significantly over the 12-month study period. However a significant interaction

existed between location and time, due to a significant decrease in percent surface cover at Jana (shallow) over time. A comparison of means further revealed that Jana (shallow) had the fewest genera, and lowest percent surface cover and volumetric cover, although there was no significant difference in volumetric cover with Jana (deep) (Table 5.3). Further, there was no significant difference in the number of genera between Jana (deep) and Abu Ali, although the inshore study site consistently had the highest cover. These trends can also be seen in a comparison of the calculated means over the 12-month study period for each site (Table 5.4). Correlation analysis was also used to further investigate temporal relationships (Table 5.4).

At Abu Ali, the algal percent cover on the settlement plate remained high throughout the study period, although a decrease was detected during late summer (Figure 5.1). A corresponding decrease in diversity was observed in terms of the total number of different genera occurring on the replicates. A total of 19 genera was recorded for the inshore community, with a maximum of 14 at any one time. However, the percent surface cover of the shallow community at the offshore study site was lower than that at Abu Ali, and exhibited a significantly negative linear relationship with time (Figure 5.3a; Table 5.4). A significant decrease was also detected in algal diversity. A total of 12 genera was recorded for the shallow offshore community, with a maximum of 8 at any one time. The deep offshore community showed a more stable percent surface cover and diversity, with a total of 13 recorded genera and a maximum of 11 at any one time (Figure 5.4a).

The composition of algal communities at each study site was determined by ranking the overall abundances of the dominant genera (Table 5.5). Overall abundance was calculated as the product of the total volumetric cover throughout the study period and the number of recorded occurrences. The inshore shallow site at Abu Ali was characterised primarily by filamentous algae (Plate 5.4); namely *Polysiphonia* and *Sphacelaria* spp., with less frequent occurrences of *Chaetomorpha*, *Herposiphonia* and *Enteromorpha* spp.. In contrast, both offshore sites were dominated by encrusting forms of algae, *?Ulvella* and *?Peyssonnelia*, where the latter was predominantly limited to the deeper site (Plate 5.4). Although less prominent, filamentous algae at the offshore site also differed from genera associated with the inshore site due to the occurrence of *Acrochaetium* and *Anotrichium* spp. and a greater abundance of *Feldmannia/Hincksia* spp.. *Polysiphonia* and *Sphacelaria* also occurred at the offshore sites, but were considerably less abundant. Interestingly, *Herposiphonia* appeared to be limited to shallow habitats as it was common to both Abu Ali and Jana (shallow) but absent from Jana (deep). Common to all sites, however, was an assemblage of microalgae consisting mainly of *Microcoleus* and *Schizothrix* spp.

The filamentous nature of the algal community at Abu Ali resulted in a larger volumetric cover than the crustose-dominated communities at Jana (Figure 5.5). Furthermore, the abundance of the inshore algal community fluctuated considerably while the offshore communities remained relatively stable throughout the study period, with Jana (deep) the being most stable. Structural and temporal

differences between the three sites can be seen more clearly from changes in abundance of the different size (i.e., height) classes (Figures 5.2, 5.3b, 5.4b). All three study sites exhibited an increased standing crop during the winter/early summer period, although the inshore community contained the largest size class (i.e., > 10 mm). Maximum height attained by the shallow and deep offshore communities was 3-6 mm (SC 3) and 1-3 mm (SC 2) respectively.

Seasonal patterns of abundance of all recorded genera listed in Table 5.5 are shown for the three study sites in Figures 5.6, 5.7 and 5.8. Microalgal assemblages were ephemeral; maximum cover occurred during late summer/autumn, but was virtually absent in winter. At Abu Ali *Polysiphonia* and *Sphacelaria* were also consistently abundant throughout the year, in addition to being the most dominant genera. Likewise at the offshore sites, the encrusting algae *?Ulvella* and *?Peyssonnelia* were also consistently abundant throughout the year. In contrast, *Polysiphonia* and *Sphacelaria* were seasonally limited to late winter/summer. *Feldmannia/Hincksia* spp. were also limited to the late winter/summer seasons for all locations, though most markedly at the offshore shallow site.

Changes in percent similarity index, based on volumetric cover for each recorded genus, revealed that the shallow inshore algal community at Abu Ali was more closely akin to the shallow offshore community at Jana rather than the deeper one. A maximum percent similarity of 61.5 % (Abu Ali vs. Jana (shallow)) and 36.5 % (Abu Ali vs. Jana (deep)) was recorded, while the shallow and deep offshore communities reached a maximum similarity of 68.3 % (Figure 5.9). Seasonal patterns were also observed. Values increased during summer, then radically decreased throughout the winter, followed by an increase again during the spring. However the higher level of similarity in the summer may have been largely attributed to the seasonal growth of microalgae (Figure 5.10).

The results of the quadrat sampling along the 50 m transect revealed that the inshore reef was successively dominated by three phaeophyte taxa (Figure 5.11). The first to appear during the winter was *Hincksia mitchellae*, followed by *Colpomenia sinuosa*, which reached maximum abundance in late winter. Finally *Sargassum* spp., having steadily increased throughout the winter, continued until its disappearance in early summer.

5.4 Discussion

5.4.1 Experimental design

The advantages of using artificial material, such as unglazed ceramic, as a settlement plate were: (i) financial and logistical, and related to this; (ii) ease in production of identical plates, both in size and surface texture (i.e. suitable as replicates). Some studies investigating epilithic algal communities have moved away from using artificial materials for settlement plates and instead mimic natural conditions

by using plates cut from coral blocks (usually from genera such as *Acropora* and *Porites*; Carpenter, 1986; Scott and Russ, 1987). However such resources were not available for the present study.

The main disadvantage of using ceramic plates is the difference in texture when compared to the natural substratum. The latter has a non-uniform, irregular surface which provides many cryptic habitats for epilithic algae. This difference is probably partially responsible for the observed preliminary results. Despite the occurrence of similar genera, relative abundances on the natural substratum and the settlement plate differed sufficiently to produce relatively low similarity estimates (c. 50-60 %; Table 5.1). However, there was also a high level of natural variability between replicates (pers. obs.) and therefore the differences between substratum types were not solely due to texture bias. Furthermore, the advantage of being able to produce numerous identical replicate plates is deemed to outweigh any disadvantages due to the use of ceramic as a settlement material.

Another possible source of bias is visual avoidance or attraction to the artificial substratum. This would mainly apply to the herbivorous reef fish. For example, Jana (shallow) showed a significant decline in percent surface cover and the number of genera occurring on the plate surfaces. These were both significantly lower than those occurring on the natural substrate and may be due to visual biases between the two substrata (i.e. preferences to graze artificial substratum).

The design of the experimental panels themselves appeared to replicate natural grazing conditions reasonably well. Ideally, each settlement plate should have been individually secured to the reef. However, given the volume of plates involved, this was not logistically feasible. However an obvious disadvantage of combining many plates onto one panel in order to create a scientifically uniform environment, is the problem of accessibility by benthic herbivores. For example, the aluminium frame surrounding the wire-based panel may have deterred some urchins from climbing onto the plates. Furthermore, due to the uneven nature of the reef substratum, a uniformly flat area large enough to contain the panel could not always be found, and hence the entire length of the panel's frame was not entirely in contact with the substratum. (Small individuals were even discovered residing underneath the panel). Hence the plates were not equally accessible from all edges of the panel. This was primarily a problem at Abu Ali, where the panels were weighted down by concrete blocks, and not secured by stakes as on the offshore study sites. Indeed, urchins were seen clustering around the concrete blocks. Whether this was due to an attraction to the blocks either for shelter or the grazing over its surface, and/or used as the easiest access point to the panels is not clear. However, urchins were seen grazing on the plates and accessibility was assumed to be normal.

Another possible disadvantage of the equipment design, at Abu Ali in particular, was that during periodically strong currents and wave action, the large surface of the wire-based panel undulated in response to the currents over the reef. This may have deterred grazing urchins from venturing across the panel, individuals preferring to stay nearer the edges. Hence grazing pressure and impact on the

algal community may not have been uniform for all replicate plates. However the grazing impact of the urchins was highly localised anyway (i.e., one tile at a time), and therefore any biases from deterred foraging behaviour were considered to be obscured by this effect.

5.4.2 Effects of seasonality and location

The epilithic algal community growing on the inshore reef was characterised by filamentous algal forms, while the offshore communities were characterised by crustose ones. Scott and Russ (1987) found a similar transition in algal composition (i.e. filamentous to crustose) between the inshore, mid- and outershelf reefs across the Great Barrier Reef. Studies have also demonstrated that under increasing grazing pressure the composition of the benthic algal community shifts from being dominated by macroalgae to crustose coralline algae, with the intermediate situation characterised by filamentous algae (reviewed by Steneck, 1988). The presence of an established algal 'turf' dominating the inshore community would therefore infer the existence of herbivores exerting sufficient grazing pressure to limit the growth of larger macrophytes, but insufficient to denude the substratum completely (Steneck, 1988; Steneck and Dethier, 1994). In contrast, both offshore communities are indicative of either inhibiting environmental conditions, or intense grazing pressure under which only crustose algae can flourish (Steneck and Dethier, 1994). The former may be relevant to the deeper offshore site where light penetration is reduced. Certainly the depth of the site was well within the photic zone, but light penetration may have been comparatively lower than on other tropical reefs at similar depths, due to the high sedimentation and turbidity experienced in the Gulf (see Chapter 4). However, at the shallow offshore site neither light limitation nor scouring from wave action (i.e. location on the island's leeward side) seemed likely. Hence it is deduced that the composition of at least the shallow offshore algal community, was maintained by a high level of grazing pressure.

In terms of structural complexity, Jana (deep) had the highest average generic algal diversity, and Abu Ali had both the highest average percent surface and volumetric cover. Jana (shallow) ranked the lowest in all cases. Considering these parameters alone, the inshore study site appeared to support an algal community more closely related to the deeper offshore study site. However the similarity indices based on the generic composition suggested that the inshore community was in fact more akin to the shallow offshore community, and that the two offshore ones were more similar to each other.

Algal cover at the inshore site declined during summer but attained maximum similarity with the shallow offshore community at this time, which was equivalent to that found between the two offshore sites. Given that the offshore communities were maintained by intense grazing pressure, it might be suggested that during the summer period the inshore study site experienced an increase in grazing pressure (i.e. an increase in herbivore abundance producing the observed decline in algal cover, see Chapter 8). However the inshore community did not undergo an increase in crustose algae, which are indicative of high levels of disturbance such as grazing (Steneck, 1988). In fact the increase in generic

similarity in the summer between all study sites was due to a seasonal growth of microalgae (Figure 5.10).

Similarly during the winter season the observed increase in algal cover at the inshore site and its reduction in generic similarity with the offshore communities might have been due to a reduction in grazing pressure (i.e. a decrease in herbivore abundance, see Chapter 8). However, the transect results clearly illustrated the seasonal succession that occurred across the inshore reef involving *Hincksia mitchellae*, *Colpomenia sinuosa* and *Sargassum boveanum*. Interestingly, while these genera were represented amongst the algal communities growing on the inshore settlement plates, their prominence was significantly lower than on the natural substratum. Furthermore, *Feldmannia* and *Hincksia* spp. were more abundant in the offshore settlement plates at this time. Colonisation on the inshore settlement plates was therefore probably being hindered.

The high sedimentation rates at the inshore site (see Chapter 4), particularly during the winter season, resulted in a layer of deposited sediment over the surface of the settlement plate. An effective barrier to algal propagules, the sediment layer would have prevented settlement and colonisation unless perturbed by grazing herbivores and consequently exposing the plate surface (Plate 5.5). This inhibition was obviously not predominant on the surrounding reef due to the topographic complexity of the natural substratum. While the settlement plate offered a uniformly flat surface, the uneven nature of the substratum ensured that some settlement space would remain uncovered. Hence the flat settlement plate probably led to higher levels of sedimentation, and possible hindrance and suppression of algal seasonal succession.

Despite certain differences between algal communities on settlement plates and the natural substratum, particularly during the winter season, the results nevertheless illustrated seasonal changes and fundamental differences between the algal communities growing on the inshore and offshore study sites.

5.4.3 Conclusions

Location, in particular distance from the shoreline, appeared to be the most important factor in determining the composition of the epilithic algal community. Seasonality, while triggering important changes, served only to change (i.e. increase or reduce) the level of similarity between the different algal communities.

However it was difficult to disassociate the effects of changing grazing pressures and the seasonality in the life-cycles of the algal genera observed. Fluctuations in grazing intensity may have been entirely responsible for the observed patterns in algal dynamics, but they may also have enhanced or hindered life-cycle effects. Further data investigating herbivore dynamics (see Chapter 8) and their differential effects (see Chapter 6) are required.

Study Site	May 1994			April 1995		
	ANOVA (2-way without replication)		% Similarity	ANOVA (2-way without replication)		% Similarity
	Genera	Substratum		Genera	Substratum	
Abu Ali	NS $p > 0.1$ ($n = 28$)	NS $p > 0.1$ ($n = 28$)	56.28	NS $p > 0.05$ ($n = 26$)	NS $p > 0.5$ ($n = 26$)	63.42
Jana (shallow)	NS $p > 0.1$ ($n = 22$)	NS $p > 0.5$ ($n = 22$)	50.00	S $p < 0.05$ ($n = 18$)	S $p < 0.01$ ($n = 18$)	57.66
Jana (deep)	NS $p > 0.1$ ($n = 18$)	NS $p > 0.1$ ($n = 18$)	61.78	NS $p > 0.05$ ($n = 22$)	NS $p > 0.1$ ($n = 22$)	62.56

Table 5.1: **ANOVA** results and **percent similarity** in terms of **percent surface cover** between the algal community growing on the natural substratum and settlement plates at the three study sites, before and after the 12-month study period. S = significant, NS = non-significant.

Study Site	May 1994			April 1995		
	ANOVA (2-way without replication)		% Similarity	ANOVA (2-way without replication)		% Similarity
	Genera	Substratum		Genera	Substratum	
Abu Ali	NS $p > 0.1$ ($n = 28$)	S $p < 0.05$ ($n = 28$)	53.25	NS $p > 0.1$ ($n = 26$)	NS $p > 0.5$ ($n = 26$)	55.06
Jana (shallow)	NS $p > 0.1$ ($n = 22$)	NS $p > 0.5$ ($n = 22$)	41.52	S $p < 0.05$ ($n = 18$)	S $p < 0.01$ ($n = 18$)	58.57
Jana (deep)	NS $p > 0.1$ ($n = 18$)	NS $p > 0.5$ ($n = 18$)	59.36	NS $p > 0.05$ ($n = 22$)	NS $p > 0.1$ ($n = 22$)	63.40

Table 5.2: **ANOVA** results and **percent similarity** in terms of total **volumetric cover** between the algal community growing on the natural substratum and settlement plates at the three study sites, before and after the 12-month study period. S = significant, NS = non-significant.

	ANOVA (2-way with replication)			**Comparison of Means** ($t_{(0\,05,23)} = 2.069$)		
	n	**Location**	**Time**	**Abu Ali vs. Jana (S)**	**Abu Ali vs. Jana (D)**	**Jana (s) vs. Jana (D)**
Log (no. genera+1)	72	S $p < 0.01$	NS $p > 0.05$	S $t = 2.232$	NS $t = 0.995$	S $t = 3.228$
Log (surface cover+1)	72	S* $p < 0.001$	S* $p < 0.001$	S $t = 5.986$	S $t = 2.136$	S $t = 3.850$
Log (volumetric cover+1)	72	S $p < 0.001$	S $p < 0.001$	S $t = 10.652$	S $t = 9.486$	NS $t = 1.166$

Table 5.3: **ANOVA** and **comparison of means** (*t*-test) results for the algal community growing on the settlement plates at the three study sites over the 12-month study period. S = significant, NS = non-significant. An asterisk (*) denotes a significant interaction term.

	Mean ± 95% confidence limits (SD parentheses)			**Correlation Analysis**		
	Abu Ali (n = 24)	**Jana (shallow)** (n = 24)	**Jana (deep)** (n = 24)	**Abu Ali** (n = 12)	**Jana (shallow)** (n = 12)	**Jana (deep)** (n = 13)
No. genera	5.33 ± 0.69 (1.63)	4.31 ± 0.76 (1.79)	5.79 ± 0.62 (1.47)	NS $p > 0.5$ r = -0.17	S $p < 0.01$ r = -0.80	NS $p > 0.5$ r = 0.12
Surface cover	84.17 ± 4.39 (10.38)	63.75 ± 6.50 (15.40)	75.50 ± 3.57 (8.45)	NS $p > 0.5$ r = -0.04	S $p < 0.001$ r = -0.86	S $p < 0.05$ r = -0.65
Volumetric cover	149.33 ± 16.08 (38.09)	76.60 ± 7.58 (17.96)	80.67 ± 3.91 (1.89)	NS $p > 0.5$ r = -0.13	S $p < 0.001$ r = -0.74	S $p < 0.05$ r = -0.75

Table 5.4: **Correlation analysis** of the algal community growing on the settlement plates at the three study sites over the 12-month study period. Means with 95 % confidence limits are also given. S = significant, NS = non-significant, SD = standard deviation.

Abu Ali		**Jana (shallow)**		**Jana (deep)**	
Genera	**%**	**Genera**	**%**	**Genera**	**%**
Polysiphonia	40.87	*?Ulvella*	35.62	*?Peyssonnelia*	40.81
Sphacelaria	33.53	Microalgae	30.98	*?Ulvella*	23.25
Microalgae	8.06	*Feldmannia/Hincksia*	25.19	Microalgae	15.22
Chaetomorpha	6.00	*Sphacelaria*	4.86	*Feldmannia/Hincksia*	5.22
Herposiphonia	3.44	*Acrochaetium*	1.27	*Acrochaetium*	4.94
Enteromorpha	1.32	*Cladophora*	0.80	*Sphacelaria*	3.76
Fosliella	1.32	*Polysiphonia*	0.75	*Polysiphonia*	2.02
Cladophora	1.08	*Herposiphonia*	0.25	*Fosliella*	1.94
Padina	0.86	*Ceramium*	0.15	*Anotrichium*	1.38
Centroceras	0.79	*Anotrichium*	0.05	*Bryopsis*	0.63
Ceramium	0.77	*Fosliella*	0.05	*Cladophora*	0.42
Phaeophyte (juv.)	0.65	*?Peyssonnelia*	0.03	*Ceramium*	0.16
Feldmannia/Hincksia	0.54			*Aglaothamnion*	0.08
?Ulvella	0.38				
Jania	0.17				
Hypnea	0.14				
Crouania	0.02				
Spyridia	0.02				
Chondria	0.02				

Table 5.5: **Ranked abundance** of all genera recorded in the algal communities growing on the settlement plates at the three study sites. The genera are listed in decreasing order of abundance based on their total volumetric cover multiplied by the number of times each genus was recorded during the 12-month study period. This relative dominance is given as a percentage of the total abundance of the community.

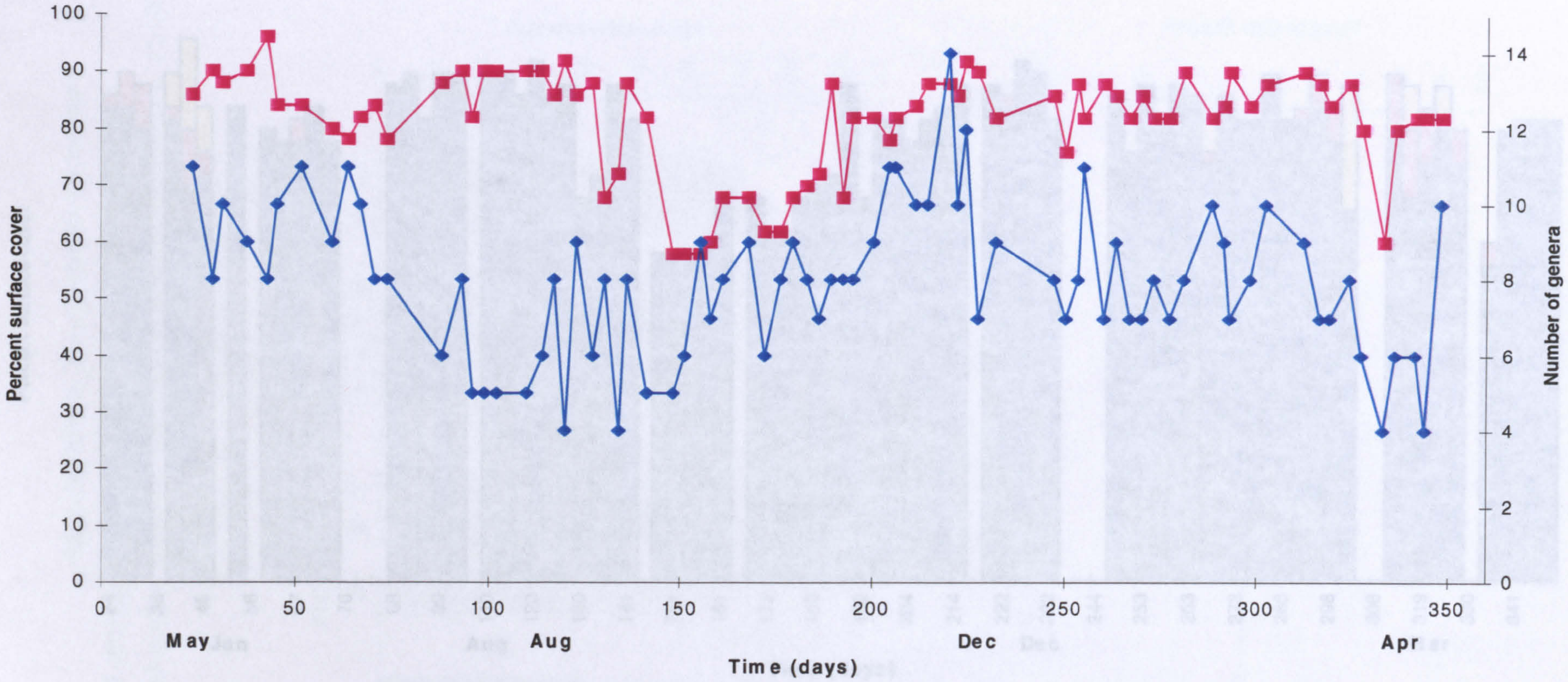


Figure 5.1: **Number of genera** (◆) and the total **percent surface cover** (■) of the algal community at **Abu Ali**.

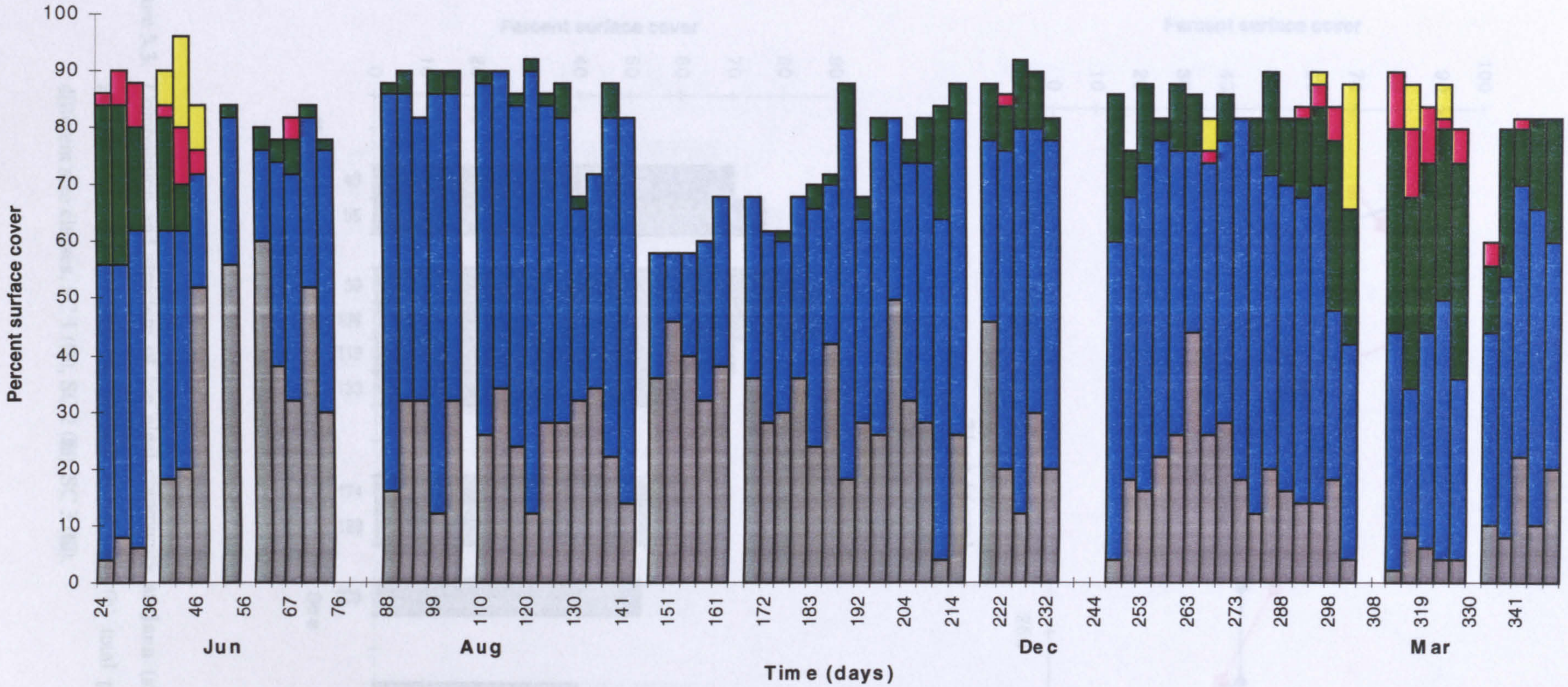


Figure 5.2: Total percent surface cover of different **size classes** (SC) of the algal community at **Abu Ali**; SC 1 (▒), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

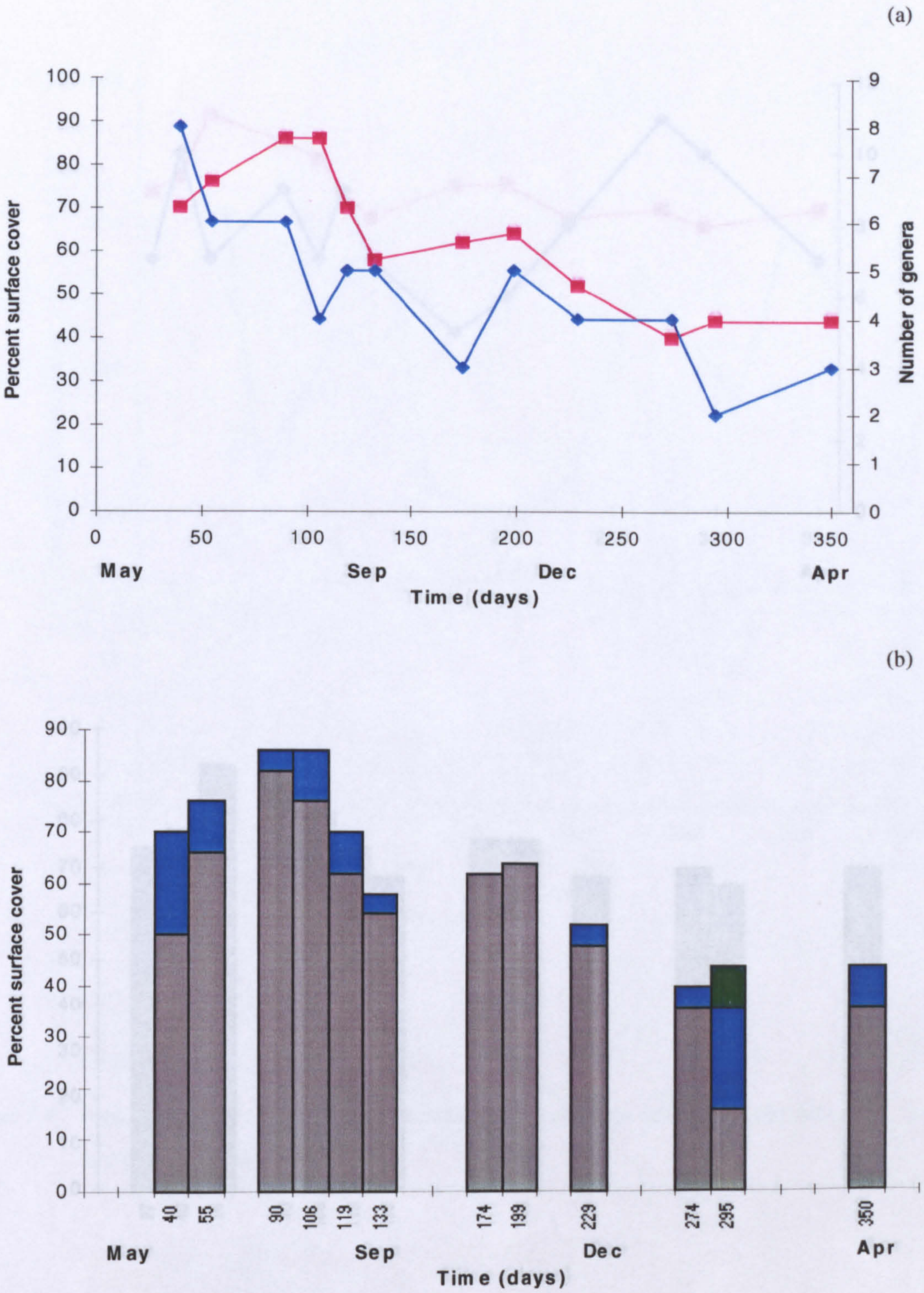


Figure 5.3: Composition and structure of the algal community at **Jana (shallow)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■).

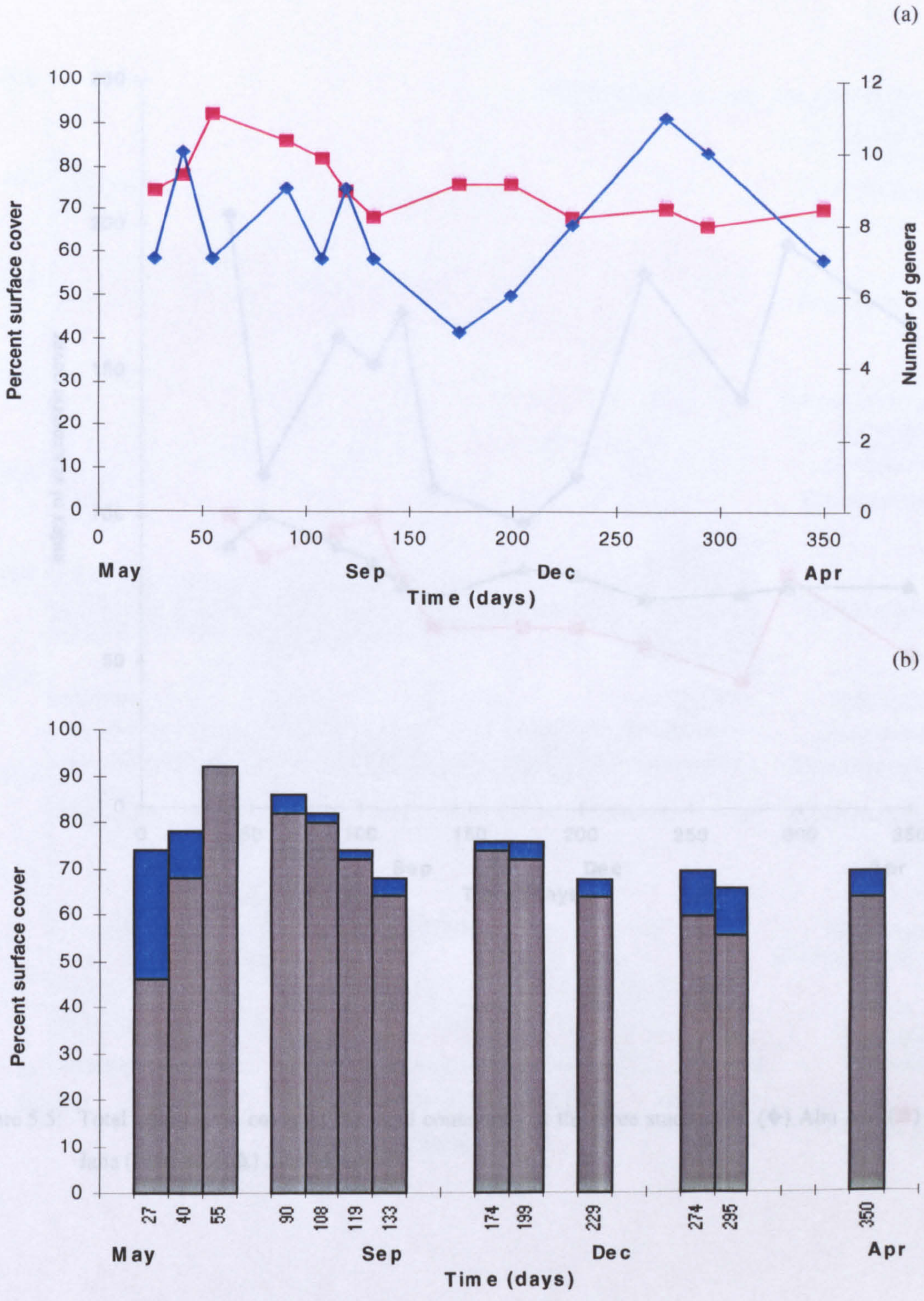


Figure 5.4: Composition and structure of the algal community at **Jana (deep)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■).

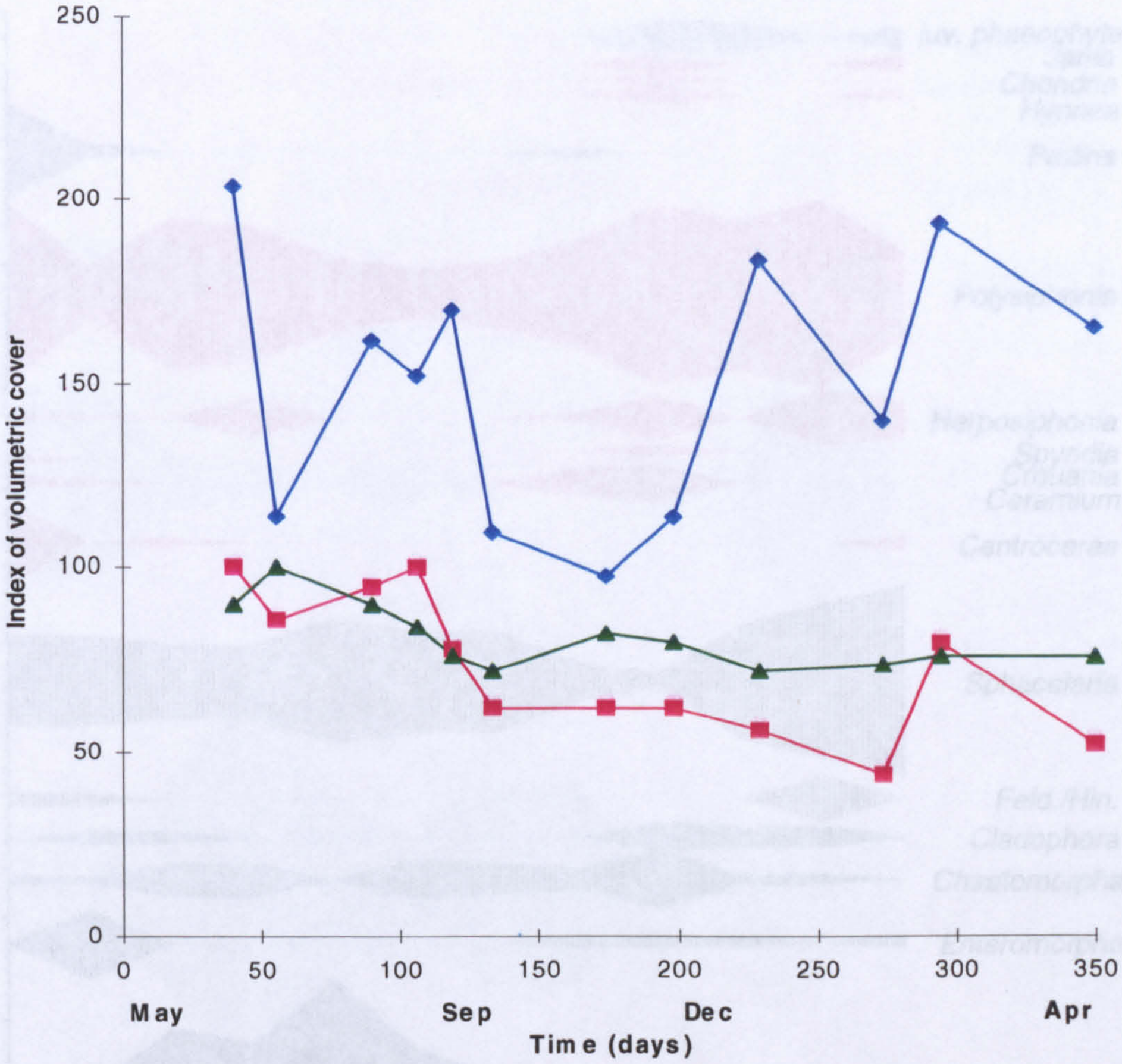


Figure 5.5: Total **volumetric cover** of the algal community at the three study sites; (◆) Abu Ali, (■) Jana (shallow), (▲) Jana (deep).

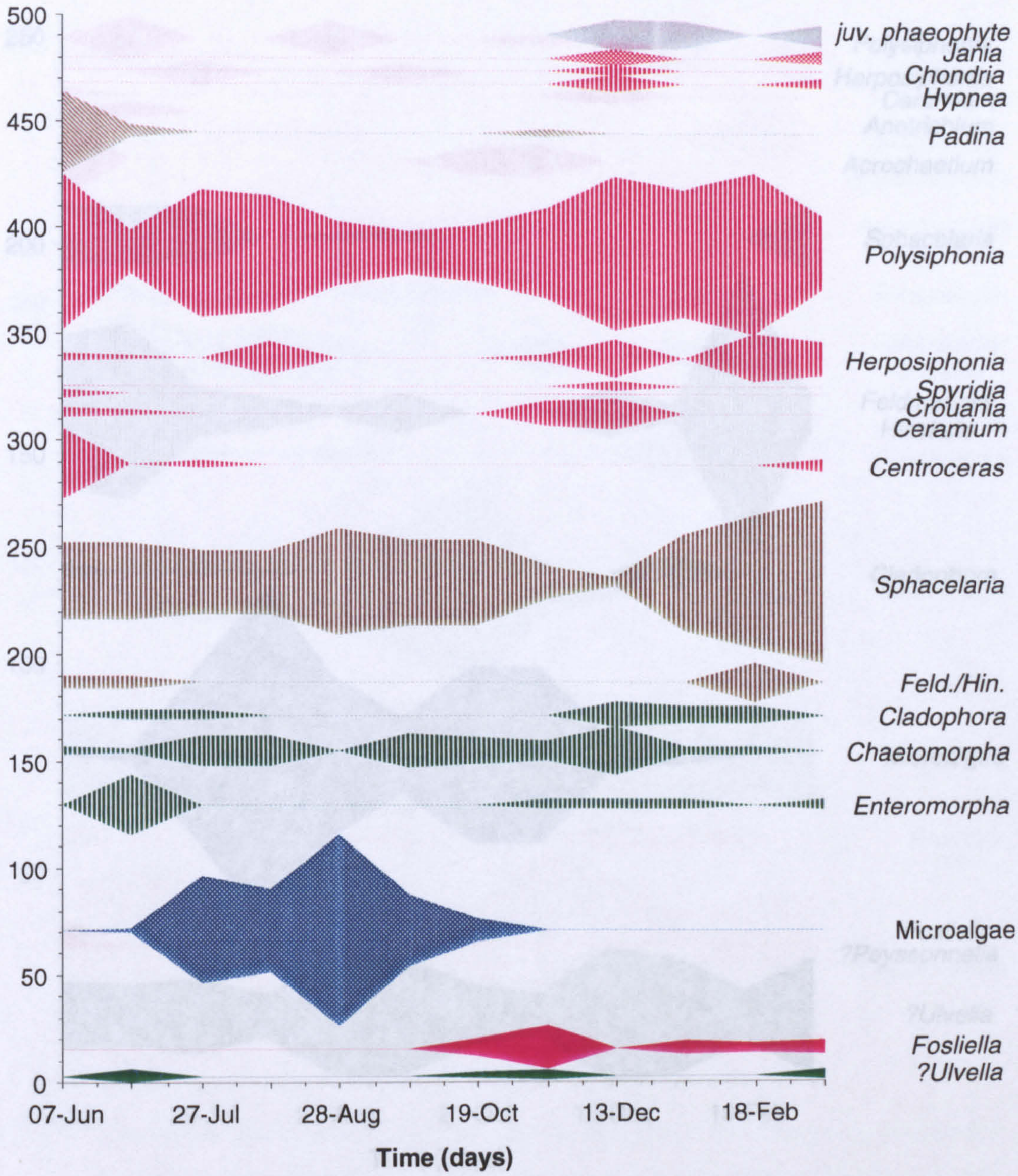


Figure 5.6: **Seasonal patterns** in total volumetric cover per genus recorded at **Abu Ali** throughout the study period;

crustose	microalgae	filamentous
corticated-foliose	corticated macrophytes	articulated calcareous
Chlorophyta	Phaeophyta	Rhodophyta

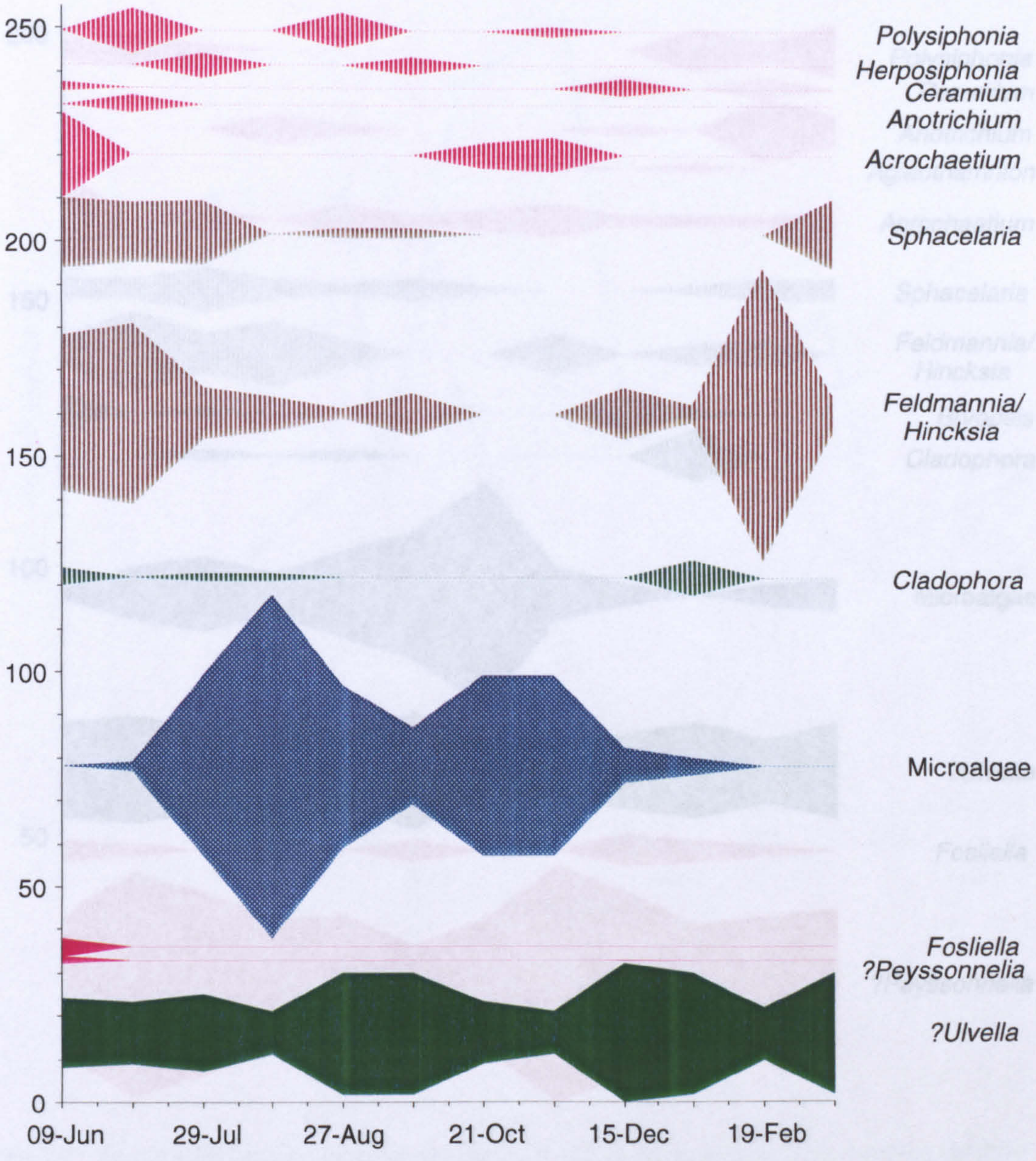


Figure 5.7: **Seasonal patterns** in total volumetric cover per genus recorded at **Jana (shallow)** throughout the study period;

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

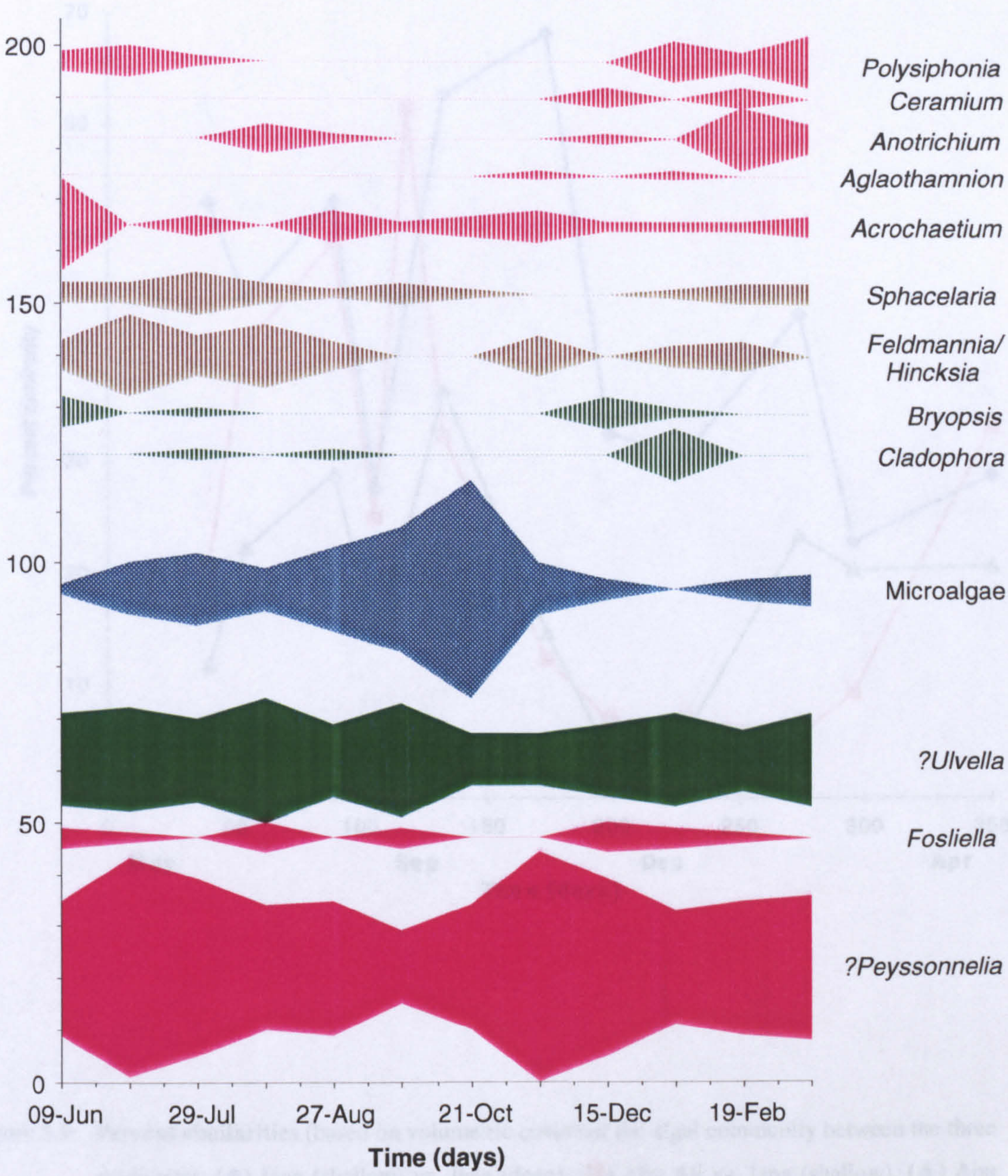


Figure 5.8: **Seasonal patterns** in total volumetric cover per genus recorded at **Jana (deep)** throughout the study period;

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

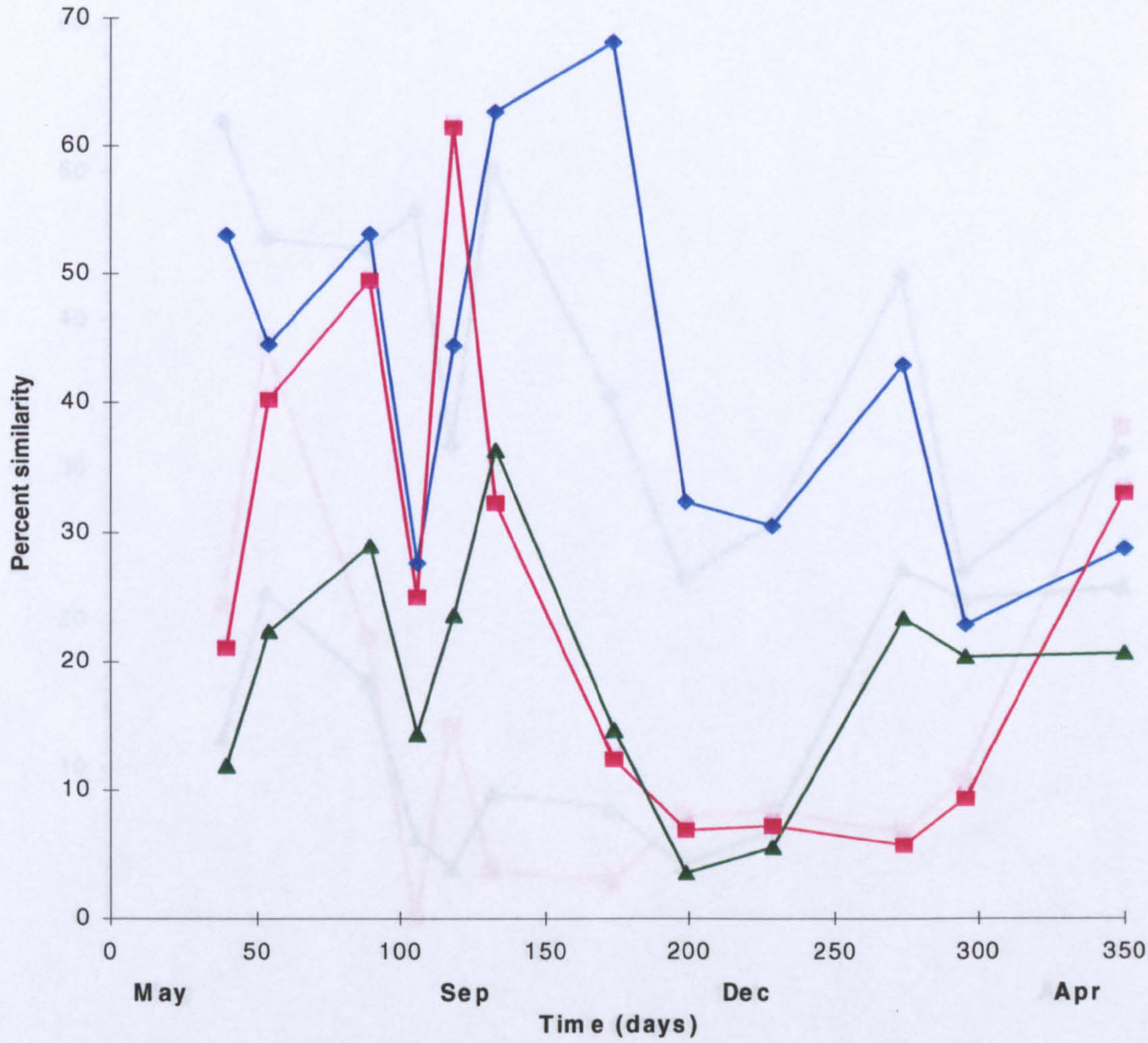


Figure 5.9: **Percent similarities** (based on volumetric cover) of the algal community between the three study sites; (◆) Jana (shallow) vs. Jana (deep), (■) Abu Ali vs. Jana (shallow), (▲) Abu Ali vs. Jana (deep).

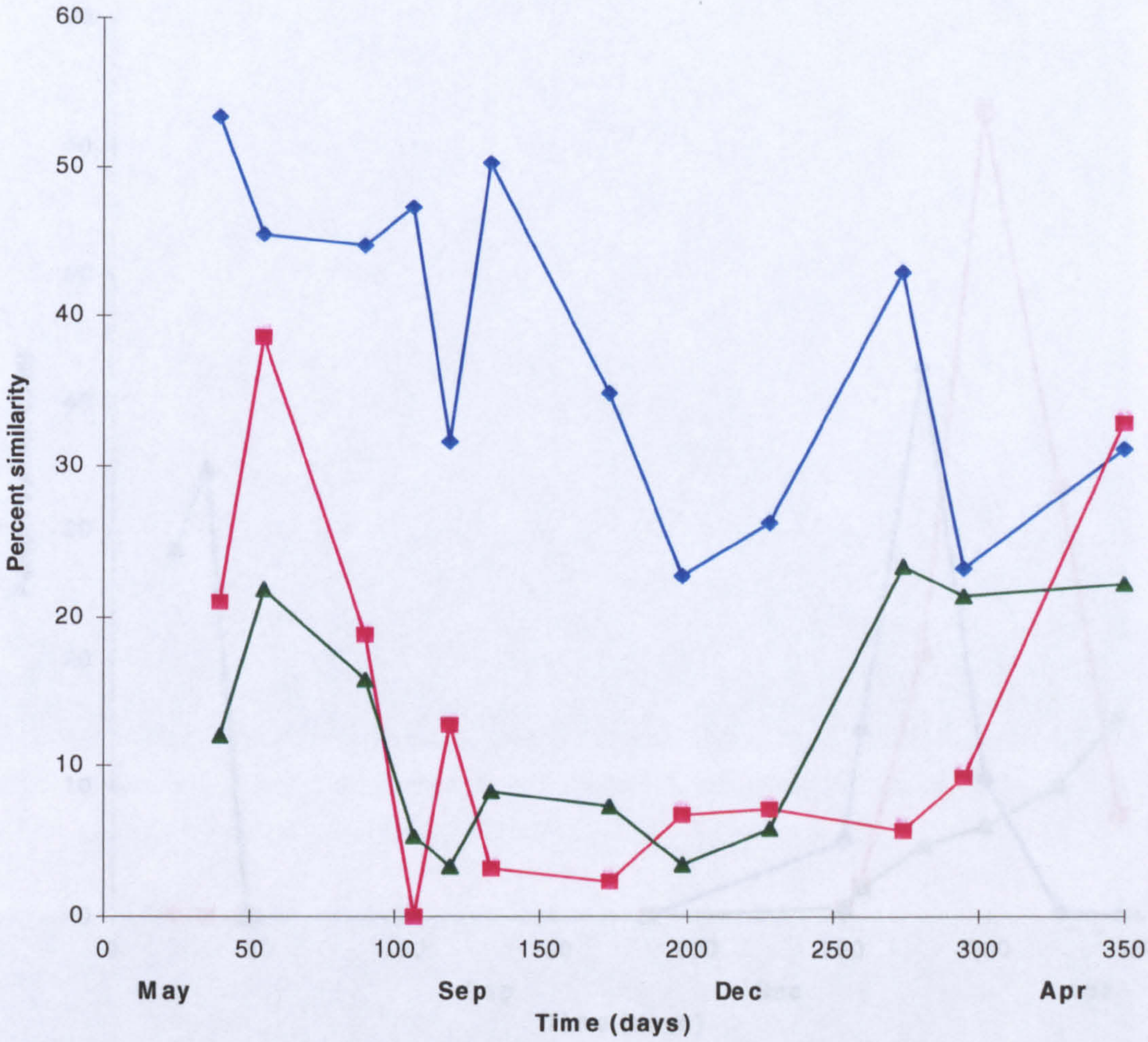


Figure 5.10: **Percent similarities** (based on volumetric cover) of the algal community between the three study sites **excluding microalgae**; (◆) Jana (shallow) vs. Jana (deep), (■) Abu Ali vs. Jana (shallow), (▲) Abu Ali vs. Jana (deep).

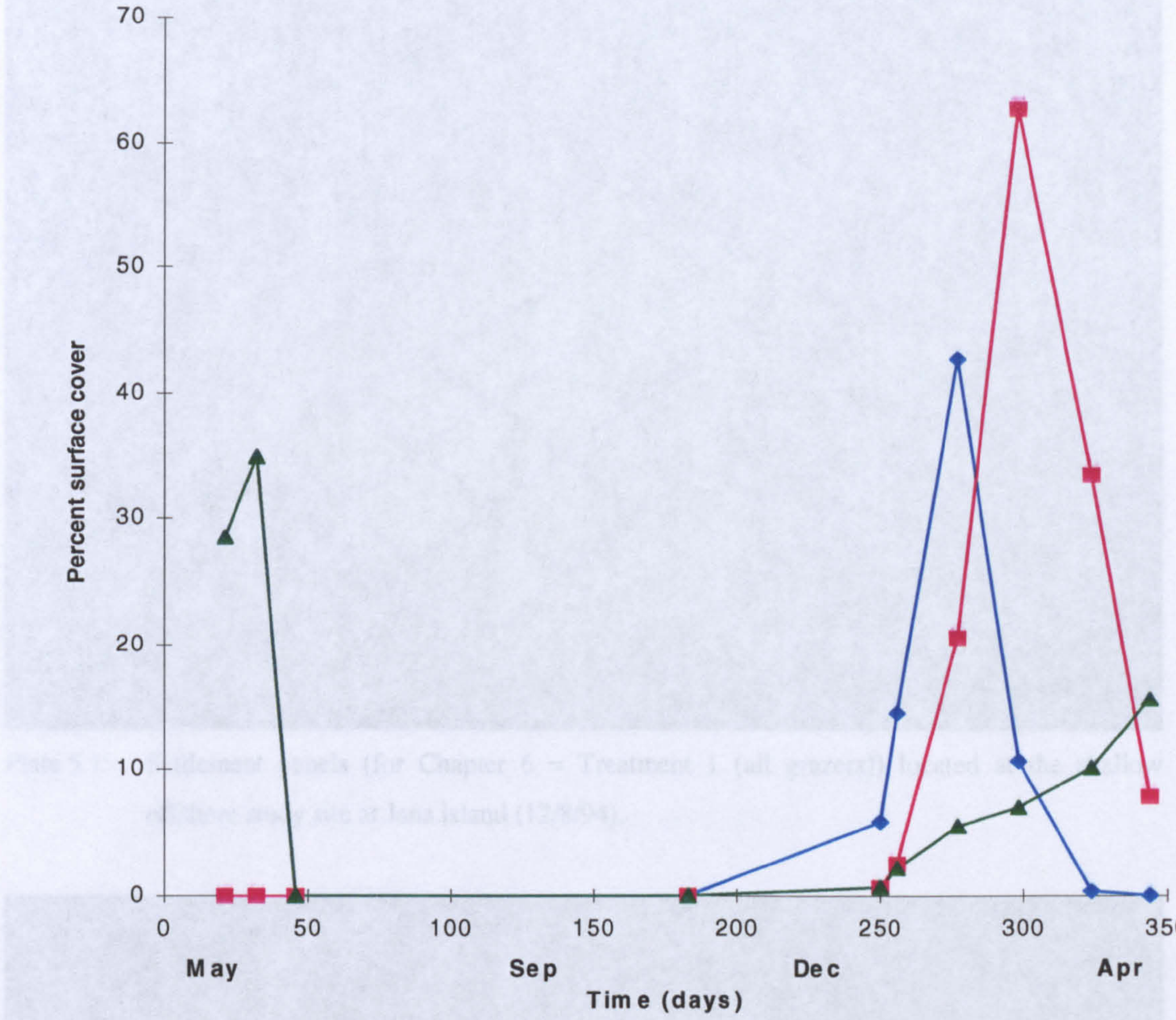


Figure 5.11: Total percent surface cover of selected **macroalgal genera** at **Abu Ali**; (◆) *Hincksia mitchellae*, (■) *Colpomenia sinuosa*, (▲) *Sargassum* spp.

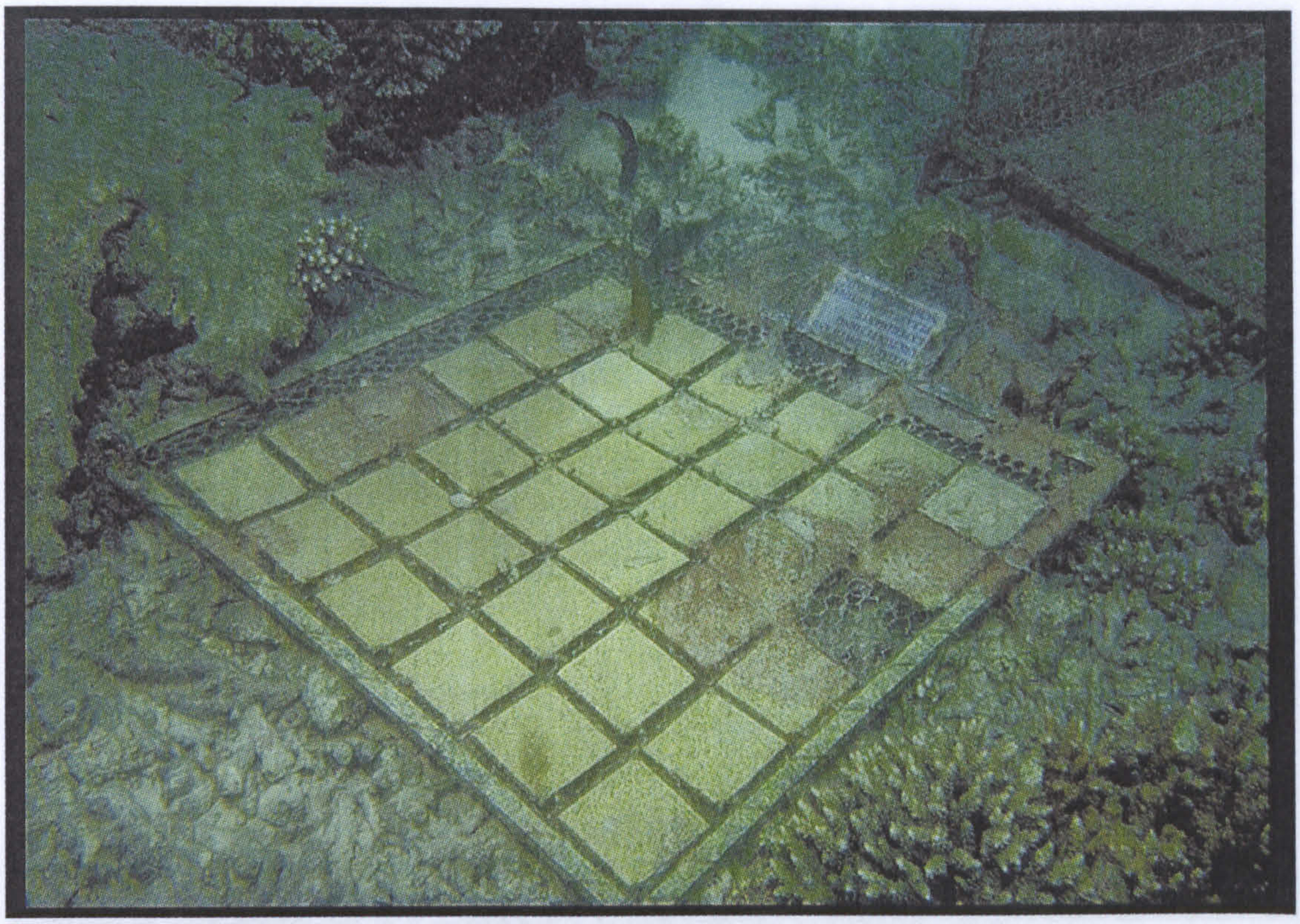


Plate 5.1: Settlement panels (for Chapter 6 = Treatment 1 (all grazers)) located at the shallow offshore study site at Jana island (12/8/94).

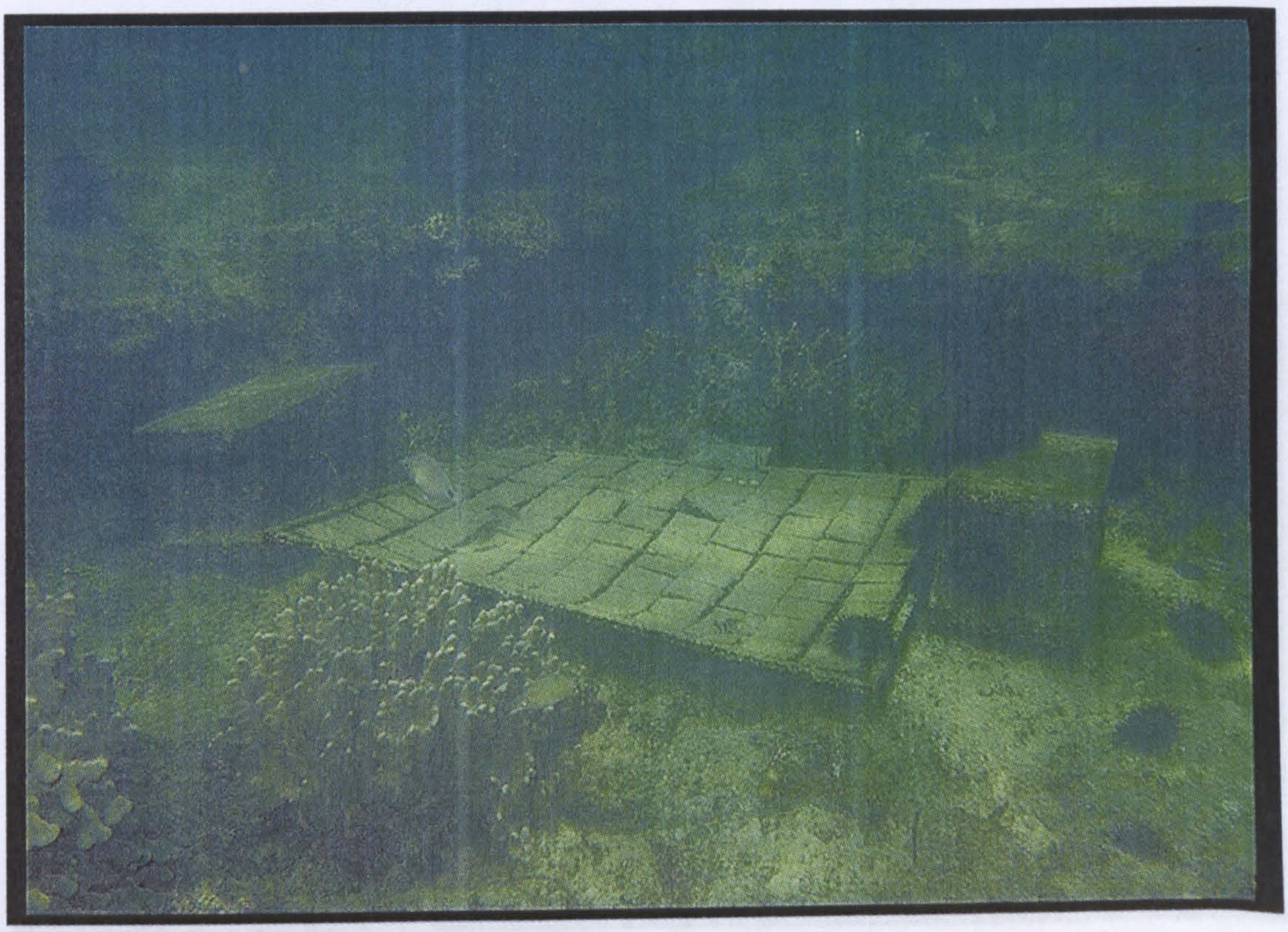


Plate 5.2: Settlement panels (for Chapter 6 = Treatment 1 (all grazers)) located at the shallow inshore study site at Abu Ali (8/94).

Plate 5.3: *Echinometra mathaei* grazing on settlement plates (for Chapter 6 = Treatment 1 (all grazers)) located at the shallow inshore study site at Abu Ali (8/94).

Plate 5.4: Settlement plates (washed) from the three study sites where, from left to right; Abu Ali (top row), Jana (shallow) and Jana (deep) (bottom row) (29/1/95).

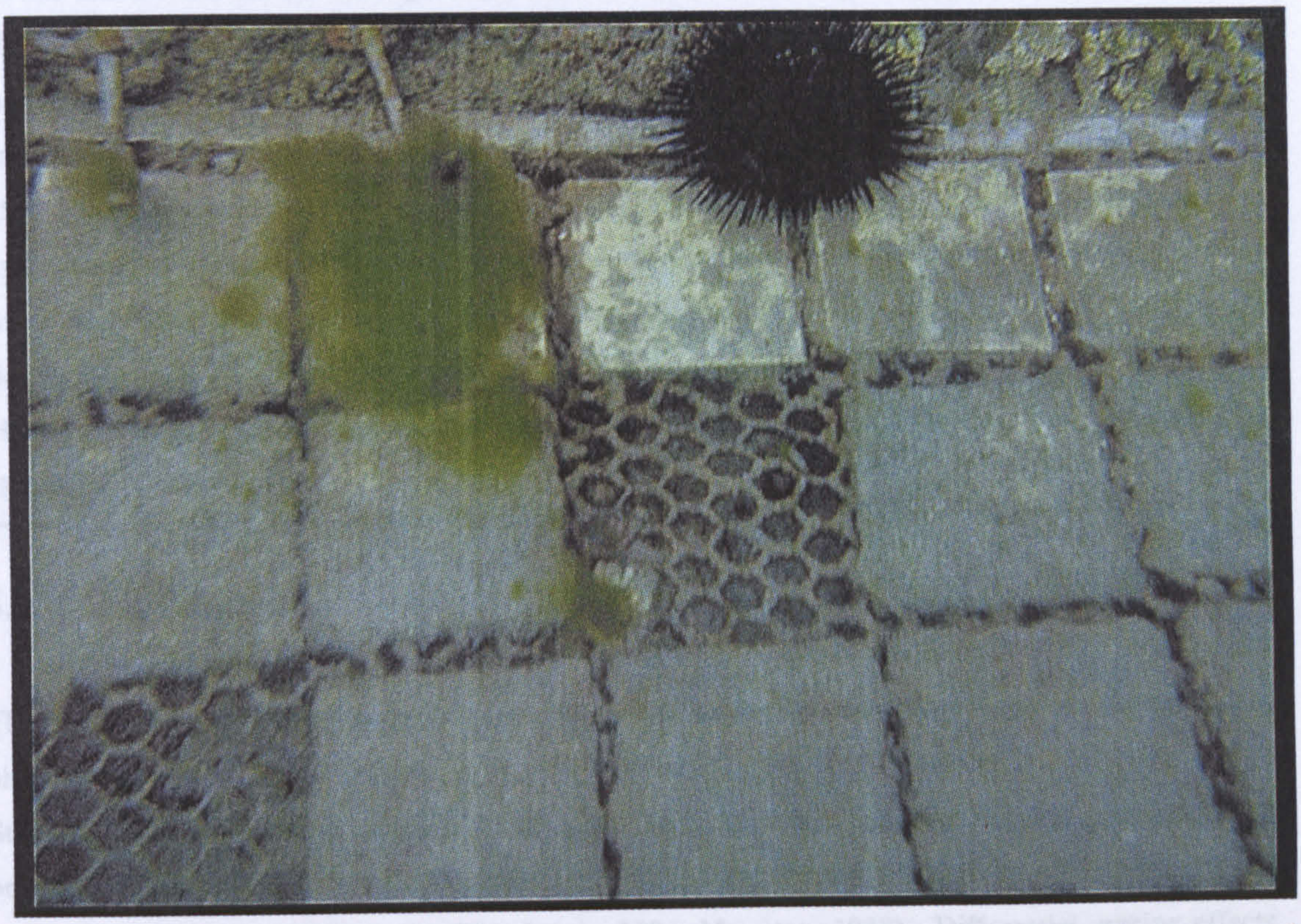


Plate 5.5: Colonisation by *Hincksia mitchellae* after exposure of the surface of the sediment-covered settlement plate by the grazing activities of *E. mathaei* (11/1/95).

Chapter Six

Effects of Herbivory

Summary

Exclusion cages were used to isolate the differential grazing effects imposed by echinoids and herbivorous fish on the epilithic algal community growing on settlement plates at the three study sites. At the inshore reef intermediate grazing pressure occurred, resulting in a predominantly filamentous algal community. Here the level of impact imposed by herbivorous fish was wide-ranging, uniform and intermediate, whereas impact from echinoids (i.e. *Echinometra mathaei* (de Blainville)) was localised and intense. The extreme grazing pressure experienced by the shallow offshore, crustose-dominated algal community was attributed to herbivorous fish only. The relative importance of herbivorous fish and urchins could not be clarified at the deep offshore site due to logistical constraints. Total exclusion of all herbivores revealed that algal biomass was highest at the shallow offshore reef, while at the deeper site algal biomass appeared limited by factors other than herbivory, such as light limitation. Hence, as a regulating factor of the epilithic algal community, herbivorous grazing was most important at the shallow offshore reef.

6.1 Introduction

Throughout the majority of coral reef ecosystems the most important biogenic factor limiting algal biomass and distribution is removal by grazing herbivores (reviews by Hatcher, 1983; Hixon, 1983; Steneck, 1988). The various members of the herbivorous reef community (i.e. fish and echinoids) have been shown to have a differential effect on composition, structure and productivity of the benthic algal community (Hay, 1984; Carpenter, 1986; Lewis, 1986; Morrison, 1988). Differential grazing effects result from spatial variation in impacts from uneven herbivore distribution and abundance (Hay, 1981a; Hay and Goertemiller, 1983; Lewis and Wainwright, 1985) and also from differing morphologies and grazing effectiveness (Ogden and Lobel, 1978; Bellwood and Choat, 1990; Purcell and Bellwood, 1993). These have further been used to classify the herbivorous community in terms of functional groups (Steneck, 1988).

Various approaches have been employed to assess the differential effects of herbivorous grazing, the most common using exclusion cages to monitor the effect of different grazing regimes on the epilithic algal community (Stephenson and Searles, 1960; Hatcher, 1981; Hixon and Brostoff, 1981; Hatcher and Larkum, 1983; Carpenter, 1986; Lewis, 1986; Scott and Russ, 1987; Morrison, 1988).

Through the use of exclusion cages, the aim of this study was to assess the relative role of different herbivore groups (i.e., fish and urchins) in regulating the epilithic algal community at the three study sites.

6.2 Materials and methods

6.2.1 Experimental design

The design of the equipment used and procedures employed are based on a study by Carpenter (1986) at St. Croix, United States Virgin Islands (USVI). In November 1993, 24 panels were equally distributed between the three study sites (Chapter 3) and covered with a total of 1376 algal settlement plates. (Their design was identical to those described in section 5.2.1). The panels were left for five months to acquire a natural growth of algae. In May 1994, the 8 panels at each site were subjected to five treatments (three replicates and two individual controls), which exposed the algal community growing on the respective settlement plates to different grazing regimes, by permitting or inhibiting access by either herbivorous fish or urchins. The settlement panels used in Chapter 5 were also incorporated into this experiment as a sixth treatment (i.e., that of unrestricted access by the different macroherbivore groups). Details of the six treatments are summarised in Table 6.1.

For Treatment 1 (Plates 5.1, 5.2), the settlement plates were left exposed throughout the whole experimental period thereby allowing uninhibited access to the algal growth by the herbivorous groups. This treatment would therefore simulate normal grazing pressure upon the epilithic algal community. In Treatment 2 (Plate 6.1), an exclusion cage was used to completely enclose the settlement plates; preventing access by either herbivorous group (i.e., fishes or urchins > 1.3 cm diameter) and allowing unimpeded growth of the algal community. Treatment 3 (Plate 6.2), allowed access to herbivorous fish only, through the use of an open-lipped cage around the settlement plates (i.e., the projecting sides of the cage preventing entrance of urchins). Conversely in Treatment 4 (Plate 6.3), a complete cage prevented grazing by herbivorous fish of greater than 1.3 cm diameter, but contained a number of urchins able to graze freely upon the plates. This urchin density within the sealed cage area matched the ambient population density of the surrounding reef (calculated from urchin population density estimates, see Chapter 8). Hence Treatments 3 and 4 would separate the relative impacts of each herbivorous group upon the algal community. Treatments 5 and 6 (Plates 6.4, 6.5) were experimental controls designed to elucidate any artificial influences occurring due to the presence of the cages. It is assumed that microherbivores had access to all treatments.

While the experimental design of the treatments was identical for both the inshore and offshore areas investigated, the number of plates involved and sizes of cages differed. At the inshore fringing reef along Abu Ali Island, each treatment contained 100 plates (arranged in a 10 x 10 grid). Each galvanised wire cage was 92 cm x 92 cm x 30 cm. The open-lipped cages had an additional overhang

of 15 cm. This was to further ensure that urchins were prevented from entering the cages. At the offshore island of Jana, each treatment contained 36 plates (arranged in a 6 x 6 grid) and each galvanised wire cage was 61.5 cm x 61.5 cm x 30 cm. Again the open-lipped cages had a 15 cm overhang. Treatments 1 to 4 were replicated at each site while Treatments 5 and 6 occurred singly. Hence at each of the three sites (one inshore, two offshore), ten treatments were located; four treatments replicated and two individual controls. Attachment of the panels and cages to the substratum at each study site was identical to the methodology described in section 5.2.1.

Monitoring of the algal community growing on the settlement plates began in May 1994 and continued for a total of twelve months. During sampling a single plate was randomly selected from each replicate panel (i.e. a total of two plates per sample), the algal community growing upon it investigated (see section 6.2.2), and then replaced in order to keep the surface area available to grazers and colonising algae constant. At the inshore site, this was undertaken twice a week, while the offshore sites plates were removed once every two weeks.

6.2.2 Sample and data analysis

The analyses performed were identical to those described in sections 5.2.2 and 5.2.3.

6.3 Results

6.3.1 Effects of caging

In order to reveal whether the presence of the exclusion cages had any bias on the growth of the algal community on the settlement plates, a statistical comparison was made between Treatment 1 and the control Treatments 5 and 6 (pooled) at each study site (Table 6.2). At Abu Ali, while there was no difference in the number of genera and the volumetric cover of the algal community between the treatments, the percent surface cover was significantly higher on the settlement plates of Treatment 1. In addition the number of genera and the percent surface cover varied significantly over time. At Jana (shallow) there was no significant difference between treatments, although there was a temporal difference for the percent surface cover. At Jana (deep), while there was no difference in the number of genera and the percent surface cover of the algal community between the treatments, the volumetric cover was significantly higher on the settlement plates of the controls. Furthermore both the number of genera and the volumetric cover varied significantly over time.

6.3.2 Effects of Herbivory

6.3.2.1 Abu Ali

After only two months, the exclusion cages at the inshore study site were damaged beyond repair by the last of the early summer season storms (Plate 6.6). Consequently data exist only for June and July 1994. Despite the curtailed time series, the results still reveal that differences had begun to develop in the composition of the algal community between caged treatments.

Effects of treatment and season

Comparison of the algal community between different treatments revealed significant spatial and temporal relationships. Treatment 2 contained significantly fewer algal genera than Treatment 1, but there was no spatial or temporal difference detected over the two month period for any of the other treatments (Table 6.3). However between Treatments 3 and 4, a significant level of interaction existed, revealing that under fish-only grazing pressure the number of genera declined over time while under urchin-only grazing it increased and remained relatively stable. In terms of percent surface cover there was no temporal difference between treatments (Table 6.4). In addition, the percent surface cover was significantly lower in Treatment 4 compared with all other treatments, and similarly in Treatment 1 compared with Treatment 2. In the latter case however, a significant interaction revealed that the percent surface cover is dependent on the length of exposure to the different grazing regimes (i.e. the exclusion of herbivores allowed unimpeded growth in Treatment 2). The volumetric cover in Treatment 2 was significantly larger than the other treatments (Table 6.5). Furthermore, Treatment 2 also significantly varied over time with Treatments 1 and 3. Again however, a significant interaction with Treatment 1 revealed that the volumetric cover is dependent on the length of exposure to the different grazing regimes

Seasonal changes under different grazing regimes

In Treatment 1, the percent surface cover remained relatively stable throughout the two month period, while the number of genera declined during July (Figure 6.1a). A total of 17 different genera were recorded, with a maximum of 11 at any one time. Treatment 2 however, showed a decline in percent surface cover during June and a corresponding increase during July (Figure 6.2a). The number of genera also rapidly declined during July. A total of 18 different genera were recorded, with a maximum of 11 at any one time. For Treatment 3, the percent surface cover remained relatively constant over the two month period, while the number of genera revealed an overall decline (Figure 6.3a). A total of 20 different genera were recorded, with a maximum of 12 at any one time. After an initially contrasting decrease and increase in Treatment 4, the percent surface cover and number of genera remained relatively stable. Similarly for Treatments 5 and 6 (pooled). A total of 16 different genera were

recorded for the former treatment, with a maximum of 11 at any one time. For the latter, a total of 21 different genera were recorded with a maximum of 12 at any one time.

The generic composition of the algal community growing in each of the treatments was determined by ranking the overall abundance of each genus (Table 6.6). Even after two months, all treatments are characterised by the same genera: *Polysiphonia*, *Sphacelaria*, *Padina* and *Chaetomorpha*. Less abundant genera included *Enteromorpha*, *Bryopsis*, *Cladophora*, microalgae, *Hypnea* and *Feldmannia/Hincksia* and *Centroceras*. Treatments 2 and 3 had developed a comparatively greater abundance of *Polysiphonia* and *Padina*, with the former exhibiting the largest profusion of *Polysiphonia* (Plate 6.7).

Except for Treatment 2, the volumetric cover of the algal communities in each of the other treatments compared favourably (Figure 6.6). Treatment 2, however, initially supported a variable but overall larger standing crop than the other treatments, which rapidly increased in size during July. This profusion of growth was subsequently lost by the end of the month when the exclusion cages were breached by storm damage, and again declined to levels associated with the other treatments. The structural and temporal differences between the treatments can be more clearly seen in terms of the different size (i.e. height) classes within the overall standing crop of the algal community (Figures 6.1b, 6.2b, 6.3b, 6.4b, 6.5b). For example in Treatment 2, the prominent growth of *Polysiphonia* correlated with a dramatic increase in canopy height (i.e. size class 5: > 10 mm). Treatments 1 and 5/6 had similar canopy structure and coverage, both of which had declined by the end of the study period. Treatment 3 however, had a continuously stratified canopy structure while the canopy in Treatment 4 was uneven throughout the two month study period.

The seasonal patterns of abundance of all recorded genera listed in Table 6.8 can be seen for all treatments (Figures 6.7, 6.8, 6.9, 6.10, 6.11). For example in Treatment 2, there was a high abundance of *Polysiphonia* which rapidly increased by mid-July (Plate 6.7). *Padina* had a sporadic pattern of abundance due to the patchy distribution of mature plants amongst settlement plates (Plate 6.8). *Sphacelaria* was abundant throughout the study period, but more so before the increased growth of *Polysiphonia*. Furthermore *Enteromorpha*, *Chaetomorpha*, *Centroceras* and *Spyridia*, while initially present, had all disappeared by the end of the study period, most probably due to obscurement and exclusion by the later profusion of *Polysiphonia*. It was evident that this dominance had been reduced to initial levels after the storm-induced breach of the exclusion cages. In Treatment 3, *Polysiphonia*, *Sphacelaria* and *Chaetomorpha* were steadily abundant throughout June and July, while *Padina* was sporadic. *Centroceras* and *Spyridia* however, were again only present during June. In contrast the abundance of *Polysiphonia* and *Sphacelaria* in both Treatments 1 and 5/6 was more patchy as again was *Padina*. However, *Chaetomorpha*, *Enteromorpha* and *Cladophora* were more abundant, especially in July. In addition, the crustose algae *?Ulvella* was also more prominent.

The percent similarity index, in terms of the volumetric cover for each recorded genus, revealed that even during the short two month period, the level of similarity between Treatment 1 and other treatments varied considerably (Figure 6.12). For example during the first month, Treatments 1 vs. 3 and 1 vs. 5/6 diverged and then re-converged by the end of the recording period. Indeed all treatments except Treatment 1 vs. 4 showed a decline in similarity during July. Overall, however, the order of closest similarity with Treatment 1 was: Treatment 5/6 (controls), Treatment 3, Treatment 4 and Treatment 2.

6.3.2.2 Jana (shallow)

The exclusion experiment at Jana (shallow) experienced some storm damage from the winter season onwards, although not as extreme as at the inshore study site. Treatments 1 and 2 have complete data sets, while the others did not survive the entire study period. Furthermore, Treatment 4 could not be implemented as only one *Diadema setosum* individual could be found in the surrounding study area. Hence the ambient population was too low to be simulated in the limited surface area of the exclusion cage.

Effects of treatment and season

Comparison of the algal community between different treatments revealed significant spatial and temporal relationships. The number of genera recorded varied significantly over time, except between Treatments 1 and 3 (Table 6.3). In addition, Treatment 3 contained significantly more genera than Treatments 1 and 2. The percent surface cover of the algal community also varied significantly over time between all treatments, and the cover in Treatment 2 was significantly larger than Treatments 1 and 3 (Table 6.4). In terms of volumetric cover, similar differences were detected between the treatments, but in contrast temporal differences were not significant (Table 6.5).

Seasonal changes under different grazing regimes

In Treatment 2, the percent surface cover revealed two maxima; one during the summer and the other during the spring (Figure 6.13). In contrast the number of genera recorded showed the opposite trend. A total of 17 different genera were recorded, with a maximum of 9 at any one time. Unfortunately only a partial data set exists for Treatment 3, which revealed a peak in percent surface cover during the summer and an overall decline in the number of genera (Figure 6.14). A total of 14 different genera were recorded, with a maximum of 11 at any one time. The percent surface cover and number of genera in the partial data set for Treatments 5 and 6 (pooled) compared favourably (Figure 6.15). Again a peak in algal cover occurred during the summer, a decline in the autumn and recovery in the winter. A total of 14 different genera were recorded, with a maximum of 11 at any one time. Details of Treatment 1 are given in Chapter 5.

The generic composition of the algal community growing in each of the treatments was determined by ranking the overall abundance of each genus (Table 6.7). All treatments, except Treatment 2, are characterised by microalgae, *Feldmannia/Hincksia* spp., and the encrusting alga, *?Ulvella*. Treatment 2 however, was dominated by *Hypnea* and *Polysiphonia* spp. Other relatively abundant genera common to all treatments included, *Sphacelaria* and *Acrochaetium*. Apart from Treatment 2, the volumetric cover of the algal community growing on the other treatments compare favourably (Figure 6.16). Treatment 2 however, exhibited two maxima, one during the summer season and the other during the spring. Structural and temporal differences between the treatments can be seen more clearly in terms of the different size (i.e. height) classes within the overall standing crop of the algal community (Figures 5.3b, 6.13b, 6.14b, 6.15b). For example in Treatment 2 the two peaks of successive growth by *Polysiphonia* and then *Hypnea* are characterised by a dramatic increase in canopy height (i.e. size class 5: > 10 mm). In contrast, both Treatments 3 and 5/6 were characterised by a low canopy height, although a maximum was attained during summer. Details of Treatment 1 are given in Chapter 5.

Seasonal patterns of abundance of all recorded genera listed in Table 6.7 can be seen for all treatments (Figures 5.7, 6.17, 6.18, 6.19). For example in Treatment 2, the algal community rapidly became dominated by *Polysiphonia* spp., which obscured growths of *Sphacelaria* and microalgae (Plate 6.9). However by early autumn, the standing crop of *Polysiphonia* had disappeared and the community was characterised by emerging growths of *Sphacelaria*, *Lobophora* and *Hypnea* (Plate 6.10), until exclusively dominated by the latter (Plate 6.11). Both Treatments 3 and 5/6 are characterised by *?Ulvella* and *Sphacelaria* throughout the study period, as well as microalgae and *Feldmannia/Hincksia*. In Treatment 3, *Sphacelaria* is the dominant phaeophyte, while in Treatment 5/6 the situation is reversed as well as an increased abundance of *Acrochaetium* and *Herposiphonia*. In both treatments, however, *Polysiphonia* is limited to a peak abundance during summer. However all treatments, though to a lesser extent for Treatment 2, experienced a summer bloom of microalgae which formed characteristic 'mats' across the surfaces of the settlement plates (Plate 6.12). Details of Treatment 1 are given in Chapter 5.

Comparison of the percent similarity index between Treatment 1 and the other treatments, in terms of the volumetric cover for each recorded genus, revealed that after an initially high level of similarity the algal community on Treatment 2 rapidly diverged and declined (Figure 6.20). Treatments 1 vs. 3 and 1 vs. 5/6 compare favourably, although both experienced a decline in the late summer season.

6.3.2.1 Jana (deep)

Not surprisingly, of the three exclusion experiments conducted, the one located at Jana (deep) did not suffer any storm damage. However, the population density of *D. setosum* at the study site was lower than anticipated (see Chapter 8). Therefore, in order to improve the simulated density-dependent

grazing pressure in Treatment 4, the two replicate panels and cages were combined to increase the surface area accessible by one caged *D. setosum* (Plate 6.13). This resulted in a simulated urchin population density of 1.35 m^{-2}. Unfortunately, during the initial stages of the experiment, the cages of Treatments 2 and 4 were also vandalised by leisure divers (July 1994). Although repaired, this breach allowed temporary access to the settlement plates by previously excluded herbivorous fish.

Effects of treatment and season

Comparison of the algal community between different treatments revealed significant spatial and temporal relationships. In terms of the number of genera occurring, there was no significant difference between all treatments (Table 6.3). Significant temporal relationships, however, did exist between Treatment 4 and all others. Furthermore, of these comparisons, those with Treatments 1 and 2 revealed a significant interaction. In both cases the number of genera declined further with increased exposure to urchin-only grazing pressure (i.e. Treatment 4). The percent surface cover varied significantly over time between all treatments (Table 6.4). In addition, the respective coverage in Treatments 2 and 4 was significantly larger and smaller between all other treatments. There was no difference between Treatments 1 and 3. Significant interactions, however, did exist in comparisons involving Treatment 4 and between Treatments 1 and 2, revealing the effect of increased exposure to the different grazing regimes; with Treatment 4, a decline in cover over time and with Treatment 2, an increase. The volumetric cover of the algal community exhibited identical spatial and temporal relationships as the percent surface cover, except that an additional significant interaction existed between Treatments 2 and 3 (Table 6.5).

Seasonal changes under different grazing regimes

For Treatment 2 both the total percent surface cover and the number of genera remained relatively constant throughout the study period, although the former did show an initial increase while both experienced a recovered decline during winter (Figure 6.21a). A total of 16 different genera were recorded, with a maximum of 10 at any one time. In Treatment 3 the total percent surface cover remained relatively constant throughout the study period, while the number of genera recorded showed an overall decline (Figure 6.22a). A total of 14 different genera were recorded, with a maximum of 12 at any one time. However in Treatment 4, both the percent surface cover and the number of genera show a definite decline after a relatively stable period in the summer months (Figure 6.23a). A total of 14 different genera were recorded, with a maximum of 11 at any one time. In contrast, the total percent surface cover in Treatments 5 and 6 (pooled) remained relatively stable throughout the study period (Figure 6.24a). The number of genera was also relatively constant, despite a slight initial decline, although generic richness was lower than in the other treatments. A total of 13 different genera were recorded, with a maximum of 13 at any one time. Details of Treatment 1 are given in Chapter 5.

The generic composition of the algal community growing in each of the treatments was determined by ranking the overall abundance for each genus (Table 6.8). All were characterised by an abundance of the encrusting genera *?Ulvella* and *?Peyssonnelia* (predominantly the latter), with highest concentrations in Treatments 1 and 5/6 (Plate 6.14). In contrast the enclosed community in Treatment 2 showed a profusion of *Acrochaetium* and *Sphacelaria*, while microalgae were the most abundant algae in Treatment 4. Other common genera included *Feldmannia/Hincksia*, *Polysiphonia* and *Bryopsis*. Due to their predominantly crustose nature, the volumetric cover of the algal community on settlement plates in Treatments 1, 3 and 5/6 are comparably equal, both spatially and temporally (Figure 6.25). Treatment 2, however, exhibited the highest volumetric cover, and Treatment 4 the lowest, both diverging from the other treatments during late summer. Structural and temporal differences between the treatments can be seen more clearly in terms of the different size (i.e. height) classes within the overall standing crop of the algal community (Figures 5.4b, 6.21b, 6.22b, 6.23b, 6.24b). For example, Treatment 2 was characterised by an increased canopy height and stratification throughout the study period. In contrast, Treatments 3 and 5/6 were characterised by a low canopy height and showed similar structure and cover, as was Treatment 4 during the summer season. However by early winter, the canopy cover in this latter treatment rapidly declined.

Seasonal patterns of abundance of all recorded genera listed in Table 6.8 can be seen for all treatments (Figures 5.8, 6.26, 6.27, 6.28, 6.29). For example in Treatment 2, although characterised by the presence of *?Ulvella* and *?Peyssonnelia*, there was also a peak in the abundance of microalgae during summer. The dominance of *Sphacelaria* and *Acrochaetium* increased during the study period with a maximum during early winter (Plate 6.15). *Feldmannia/Hincksia* exhibited the reverse, while *Polysiphonia* was only present during the spring and summer seasons. Treatment 3 showed similar patterns, but the size of standing crop for *Sphacelaria*, *Feldmannia/Hincksia* and *Acrochaetium* was not so pronounced, particularly for the latter. Consequently the reverse was true for the crustose algae, *?Ulvella* and *?Peyssonnelia*. Treatment 4 showed similar patterns and initial levels of abundance to Treatment 3 (Plate 6.16), but by early winter overall algal cover declined, even for the encrusting forms (Plate 6.17). Treatment 5/6 also showed similar patterns and abundance of algal genera to Treatment 3, except for a general paucity of *Polysiphonia* and patchy coverage by *Acrochaetium*. Details of Treatment 1 are given in Chapter 5.

Comparison of the percent similarity index between Treatment 1 and other treatments, in terms of the volumetric cover for each recorded genus, revealed that after an initially high level of similarity the various algal treatments rapidly diverged (Figure 6.30). Overall the similarity between Treatment 1 and other treatments declined during autumn and winter, except for Treatment 1 vs. 2 where the change occurred earlier, in the late summer. Indeed for the other treatments this was the period for maximum similarity with Treatment 1. Only Treatment 1 vs. 5/6 re-attained previous levels and being the experimental controls, Treatment 5/6 were intuitively the closest to Treatment 1. Treatment 1 vs. 3 was closer than Treatment 1 vs. 4 and overall, the least similar comparison was with Treatment 2.

6.4 Discussion

6.4.1 Experimental Design

Studies involving exclusion cages have shown that potential biases can develop due to the physical presence of the cages themselves, for example by restricting water flow and increasing sedimentation, both of which can be compounded by the growth of epiphytes over the cage surface introducing a further problem of over-shading of the settlement plates (Kennelly, 1983). All treatments were regularly cleaned throughout the present study. Also the control treatments, based on designs by Carpenter (1986), isolated the possible effects of restricted water flow from the sides (Treatment 5) and over-shading from the top (Treatment 6). Overall there was no significant difference in algal community structure between the control treatments and Treatment 1 (all grazers), apart from minor significant differences in percent surface cover at Abu Ali, and volumetric cover at Jana (deep). While these may have been due to caging effects, it is concluded that such impacts were negligible. Furthermore, the similarities in algal composition between all treatments revealed that at each study site Treatments 5/6 (control) were most akin to Treatment 1, as might be expected.

Another possible source of variability in the results was the patchy coverage of some of the recorded algae. For example, the different levels of growth across the settlement plates were apparent in Treatment 2 (Plates 6.18, 6.19, 6.20). This variance could have been reduced by increasing the number of replicate plates examined during each sampling period. However, the trade-off in the experimental design was between the sampling frequency throughout the study period and the number of replicates sampled. Logistical constraints prevented an increase in the number of replicates taken per treatment. It was assumed that the random and high frequency of sampling of the plates throughout the study period eliminated the most of the variability, and that actual trends in the changes of the community composition and structure imposed by the treatment regime were determined. Other possible biases due to the use of artificial substratum are discussed in Chapter 5.

6.4.2 Effects of differential exclusion

(a) Abu Ali

The short period (2 months) of experimental manipulation was probably insufficient to reveal any seasonal differences in community composition. As a result, all treatments included vestiges of the spring/early summer bloom of macroalgae, such as *Padina*. Its patchy distribution, however, resulted in variable levels of similarity between treatments over the study period. In the case of Treatment 2 (no grazers), the *Padina* community was superseded by a large growth of *Polysiphonia*. However, *Padina* did continue to flourish in Treatment 2, while on the other treatments this alga had almost disappeared

by the end of July. This may have primarily been a seasonal response and/or a response to an increased grazing pressure (see Chapter 8).

Studies have demonstrated that under increasing grazing pressure the composition of the benthic algal community shifts from being dominated by macroalgae to crustose coralline algae, with the intermediate position characterised by filamentous algae (reviewed by Steneck, 1988). It is therefore suggested that Treatment 3, (fish-only grazing) did not experience an intensive grazing pressure. In terms of community structure, it represented an intermediate position between Treatments 1 and 2. However, the composition of Treatment 3 was more akin to that in Treatment 2, due to the increased presence of *Polysiphonia* and *Padina*.

In contrast, Treatment 4 experienced more intensive grazing pressure, as evidenced by the lower dominance by *Polysiphonia*, the increased abundance of the crustose alga, *?Ulvella*, and the significantly lower percent surface cover (i.e. higher number of 'bare' areas of plate surface). However, this effect was not uniform across all plates within the treatment area, as some settlement plates supported large standing crops of *Polysiphonia*, characteristic of grazer-exclusion. Hence the grazing activity of *Echinometra mathaei* within Treatment 4 was slow, localised but of high impact (Plates 6.7, 6.21). Other plates not yet grazed were effectively subjected to Treatment 2 effects.

Hence the two herbivorous groups imposed different spatial and temporal levels of grazing pressure. Herbivorous fish imposed a uniform, but low level of grazing impact, which with their high degree of manoeuvrability allowed them to graze over large areas relatively quickly. In contrast, the herbivorous urchins imposed a higher level of impact, but had less manoeuvrability which resulted in localised effects (Plate 6.22).

(b) Jana (shallow)

An important seasonal event at the shallow offshore site was the summer bloom of microalgae that appeared as tightly weaved 'mats' and covered large surface areas of the substratum, including the settlement plates. This algal cover, however, was patchy and responsible for the observed fluctuations in percent similarity between treatments during summer (i.e. Treatments 3 and 5/6). In addition, these microalgal mats did not reveal signs of grazing damage and may actually be unpalatable to herbivorous fish. However, algal deterrence has usually involved corticated, leathery and calcified forms of macroalgae (Littler *et al.*, 1983; Duffy and Paul, 1992; Hay *et al.*, 1994). Furthermore, the algal community beneath the microalgae was probably inhibited by reduced light levels and increased sediment entrapment, possibly to lethal effect (reviewed by Hatcher, 1983).

The total exclusion of grazers by Treatment 2 allowed unimpeded growth and subsequent dominance by *Polysiphonia* and *Hypnea*. The reported loss of the *Polysiphonia* standing crop during late summer

may have been a seasonal effect as the other treatments also revealed a similar decline in the abundance the filamentous alga at this time. However it may have also involved sloughing in response to increased resistance to water currents and/or the production of anoxic conditions and tissue degradation at the settlement plate surface. Sloughing of large algal standing crops has been observed in other experiments involving the long-term exclusion of herbivores (Stephenson and Searles, 1960; Wanders, 1977; Carpenter, 1986).

The algal communities growing on Treatment 3 and Treatment 1 were similar, with both being dominated by the crustose alga, *?Ulvella*. Steneck and Dethier (1994) have shown that when environmental conditions are not limiting (i.e. reduced light levels with depth or scouring from strong wave action), a crustose-dominated algal community is indicative of intense grazing pressure. Since grazing activity by echinoids was not observed, it is probable that herbivorous fish exerted the majority of the grazing pressure at the shallow offshore study site.

(c) Jana (deep)

In Treatment 2, exclusion of both fish and echinoid herbivores produced the highest levels of algal biomass in terms of surface and volumetric cover (mainly *Sphacelaria* and *Acrochaetium* spp.). In contrast, Treatment 4 (urchin-only) supported the lowest coverage, while Treatment 3 (fish-only) held the intermediate position. Treatments 1 and 3 were most comparable due to dominance by crustose algal forms, which has been linked to intense grazing pressure (see above; Steneck, 1988). Hence it could be deduced that herbivorous fish exerted the majority of the grazing pressure. However Treatment 4 contained the lowest algal cover including crustose algae. This community structure implied even higher levels of grazing pressure than those experienced in Treatments 1 and 3. Since Treatment 1 was assumed to simulate grazing pressure by both fish and urchins, the level of urchin-induced grazing intensity experienced in Treatment 4 was greater than natural conditions. This was probably due to an overestimate of the ambient urchin population density (Chapter 8) compared with that simulated within the exclusion cage (i.e. 1.35 m^{-2}).

6.4.3 Effects of herbivory

The effect of total exclusion of herbivores from the epilithic algal community is well-documented (reviewed by Hatcher, 1983; Hixon, 1983; Steneck, 1988). Short-term exclusion triggers an increase in algal biomass but long-term exclusion can lead to dominance by a few macroalgal genera and possible tissue loss due to sloughing. In the present study, the exclusion-induced increase in algal biomass (i.e. Treatment 2) for the offshore communities was significantly larger at the shallow offshore site than the deep offshore site. The two communities also differed in composition; the latter was dominated by *Sphacelaria* and *Acrochaetium*, and the former successively by *Polysiphonia* and *Hypnea*. Hence, in addition to herbivory, other factors must have limited the algal community at the deep site, because the

amount of algal biomass produced under herbivore exclusion did not equal that attained by the shallow community. The most probable explanation is reduced light penetration at the deep site which would have limited the photosynthetic activity of the benthic algae (Larkum, 1983). Furthermore, under these conditions, *Sphacelaria* and *Acrochaetium* were possibly competitively superior to *Polysiphonia* and *Hypnea*, assuming equal chances of colonisation.

Direct comparison of the changes in algal cover and biomass between the inshore and offshore communities was not feasible, as both offshore communities (i.e. shallow and deep sites) were excluded from herbivores for a longer period and also experienced reduced wave action (Chapter 3). However, as explained in Chapter 5, the predominantly filamentous algal community at the inshore site compared to the crustose-dominated offshore community was indicative of a lower grazing intensity at the inshore site. A similar conclusion was reached by Scott and Russ (1987) in their comparison of the epilithic algal community growing on inshore and offshore reefs of the Great Barrier Reef. Furthermore in the present study, *Polysiphonia* was a dominant member of the inshore community and its appearance in the exclusion treatment at the shallow offshore site further supports the hypothesis. Hence, compared to the herbivorous fish community at the shallow offshore site, the combined effects of urchin and fish grazing at the inshore site were insufficient to reduce production of algal biomass and maintain a crustose community.

Other studies have also shown that herbivorous fish alone are capable of reducing algal biomass and maintaining a low standing crop (Hatcher, 1981; Hixon and Brostoff, 1981; Montgomery *et al.*, 1980; review by Hixon, 1983; Lewis, 1986). At the inshore site, herbivorous fish appeared to impose a uniform, but low level of grazing impact, while *E. mathaei* imposed a more localised, higher level of impact. At the deep offshore site the relative effects of herbivorous fish and urchins were not clear. Other studies examining the relative importance of herbivorous fish and urchins have found that the situation varies from reef to reef. For example, in the Caribbean Carpenter (1986) found *D. antillarum* to be the dominant herbivore, while Morrison (1988) found that this dominance was only applicable to shallow reefs, as herbivorous fish were the principal grazers in deeper areas. In addition, Hay (1981a) found urchin grazing to be negligible and that herbivorous fish alone were responsible for the removal of algal biomass, with highest grazing intensity recorded on the shallow reefs. However, Hay (1984) illustrated how the studies on Caribbean reefs are strongly influenced by anthropogenic effects, particularly over-fishing. His survey of previous studies clearly showed that where over-fishing had occurred, grazing urchins (i.e. *D. antillarum*) were dominant, while on unfished reefs, herbivorous fish were the dominant grazers. Furthermore the strength of competition between the two herbivore groups was demonstrated by Hay and Taylor (1985); removal of *D. antillarum* triggered a significant increase in the abundance of herbivorous fish.

It is clear therefore that the relative impact and importance of herbivorous groups differs between coral reef systems. This was also apparent between reef sites in the present study, due to the observed

differences in algal communities under different grazing regimes. However, whether these differences were due to selective feeding behaviour by the same herbivores, or differences in the composition of the herbivorous community (see Chapter 8) at each site, is discussed in Chapter 11.

Treatment	Function/Accessibility	Design
1	All grazers	No cage
2	No grazers	Closed cage
3	Herbivorous fish only	Open-lipped cage
4	Urchins only	Closed cage containing urchins of appropriate density
5	All grazers (control)	Open, three-sided cage
6	All grazers (control)	Open, one-sided cage with top

Table 6.1: Six treatments of exclusion cages, based on the experimental designs by Carpenter (1986).

	Abu Ali		Jana (shallow)		Jana (deep)	
	ANOVA (2-way with replication) ($n = 40$)		**ANOVA** (2-way with replication) ($n = 24$)		**ANOVA** (2-way with replication) ($n = 52$)	
	Treatment	**Time**	**Treatment**	**Time**	**Treatment**	**Time**
No. Genera	NS $p > 0.5$	S $p < 0.05$	NS $p > 0.5$	NS $p > 0.1$	NS $p > 0.5$	S $p < 0.05$
Surface Cover	S $p < 0.01$	S $p < 0.05$	NS $p > 0.5$	S $p < 0.05$	S $p < 0.01$	S $p < 0.001$
Volumetric Cover	NS $p > 0.1$	NS $p > 0.5$	NS $p > 0.1$	NS $p > 0.1$	S $p < 0.05$	S $p < 0.05$

Table 6.2: **ANOVA** results for the comparison of algal community growing on the settlement plates from Treatments 1 and 5/6 at the three study sites over the 12-month study period. S = significant, NS = non-significant. The interaction term was non-significant in all cases.

	Abu Ali		Jana (shallow)		Jana (deep)	
	ANOVA (2-way with replication) ($n = 40$)		**ANOVA** (2-way with replication) ($n = 24$)		**ANOVA** (2-way with replication) ($n = 52$)	
	Treatment	**Time**	**Treatment**	**Time**	**Treatment**	**Time**
ALL	S* $p < 0.01$ ($n = 100$)	S* $p < 0.05$ ($n = 100$)	S $p < 0.05$ ($n = 48$)	S $p < 0.001$ ($n = 48$)	NS $p > 0.1$ ($n = 130$)	S $p < 0.001$ ($n = 130$)
T1 vs. T2	S $p < 0.05$	NS $p > 0.05$	NS $p > 0.5$	S $p < 0.05$	NS $p > 0.05$	NS $p > 0.5$
T1 vs. T3	NS $p > 0.1$	NS $p > 0.1$	S $p < 0.05$	NS $p > 0.05$	NS $p > 0.05$	NS $p > 0.1$
T1 vs. T4	NS $p > 0.1$	NS $p > 0.5$	n/a	n/a	NS* $p > 0.5$	S* $p < 0.05$
T2 vs. T3	NS $p > 0.05$	NS $p > 0.05$	S $p < 0.01$	S $p < 0.01$	NS $p > 0.5$	NS $p > 0.5$
T2 vs. T4	NS $p > 0.05$	NS $p > 0.05$	n/a	n/a	NS* $p > 0.1$	S* $p < 0.01$
T3 vs. T4	NS* $p > 0.5$	NS* $p > 0.1$	n/a	n/a	NS $p > 0.1$	S $p < 0.05$

Table 6.3: **ANOVA** results for the comparison of the **number of genera** growing on the settlement plates between all treatments at the three study sites over the 12-month study period. S = significant, NS = non-significant. An asterisk (*) indicates a significant interaction term ($p < 0.05$).

	Abu Ali		**Jana (shallow)**		**Jana (deep)**	
	ANOVA (2-way with replication) ($n = 40$)		**ANOVA** (2-way with replication) ($n = 24$)		**ANOVA** (2-way with replication) ($n = 52$)	
	Treatment	**Time**	**Treatment**	**Time**	**Treatment**	**Time**
ALL	S $p < 0.001$ ($n = 100$)	NS $p > 0.05$ ($n = 100$)	S $p < 0.001$ ($n = 48$)	S $p < 0.001$ ($n = 48$)	S* $p < 0.001$ ($n = 130$)	S* $p < 0.001$ ($n = 130$)
T1 vs. T2	S* $p < 0.05$	NS* $p > 0.1$	S $p < 0.001$	S $p < 0.05$	S* $p < 0.001$	S* $p < 0.001$
T1 vs. T3	NS $p > 0.5$	NS $p > 0.1$	NS $p > 0.5$	S $p < 0.05$	NS $p > 0.5$	S $p < 0.001$
T1 vs. T4	S $p < 0.01$	NS $p > 0.1$	n/a	n/a	S* $p < 0.001$	S* $p < 0.001$
T2 vs. T3	NS $p > 0.1$	NS $p > 0.1$	S $p < 0.001$	S $p < 0.001$	S $p < 0.001$	S $p < 0.001$
T2 vs. T4	S $p < 0.001$	NS $p > 0.1$	n/a	n/a	S* $p < 0.001$	S* $p < 0.001$
T3 vs. T4	S $p < 0.01$	NS $p > 0.1$	n/a	n/a	S* $p < 0.001$	S* $p < 0.001$

Table 6.4: **ANOVA** results for the comparison of the **percent surface cover** growing on the settlement plates between all treatments at the three study sites over the 12-month study period. S = significant, NS = non-significant. An asterisk (*) indicates a significant interaction term ($p < 0.05$).

	Abu Ali		Jana (shallow)		Jana (deep)	
	ANOVA (2-way with replication) ($n = 40$)		**ANOVA** (2-way with replication) ($n = 24$)		**ANOVA** (2-way with replication) ($n = 52$)	
	Treatment	**Time**	**Treatment**	**Time**	**Treatment**	**Time**
ALL	S $p < 0.001$ ($n = 100$)	S $p < 0.05$ ($n = 100$)	S $p < 0.001$ ($n = 48$)	NS $p > 0.1$ ($n = 48$)	S* $p < 0.001$ ($n = 130$)	S* $p < 0.001$ ($n = 130$)
T1 vs. T2	S* $p < 0.001$	S* $p < 0.01$	S $p < 0.01$	NS $p > 0.1$	S* $p < 0.001$	S* $p < 0.001$
T1 vs. T3	NS $p > 0.05$	NS $p > 0.1$	NS $p > 0.5$	NS $p > 0.1$	NS $p > 0.05$	S $p < 0.001$
T1 vs. T4	NS $p > 0.5$	NS $p > 0.5$	n/a	n/a	S* $p < 0.01$	S* $p < 0.001$
T2 vs. T3	S $p < 0.001$	S $p < 0.05$	S $p < 0.01$	NS $p > 0.1$	S* $p < 0.001$	S* $p < 0.001$
T2 vs. T4	S $p < 0.001$	NS $p > 0.1$	n/a	n/a	S* $p < 0.001$	S* $p < 0.001$
T3 vs. T4	NS $p > 0.1$	NS $p > 0.5$	n/a	n/a	S* $p < 0.001$	S* $p < 0.001$

Table 6.5: **ANOVA** results for the comparison of the **volumetric cover** growing on the settlement plates between all treatments at the three study sites over the 12-month study period. S = significant, NS = non-significant. An asterisk (*) indicates a significant interaction term ($p < 0.05$).

Treatment 1		Treatment 2		Treatment 3		Treatment 4		Treatments 5 & 6	
Genera	**%**	**Genera**	**%**	**Genera**	**%**	**Genera**	**%**	**Genera**	**%**
Sphacelaria	33.89	*Polysiphonia*	61.81	*Polysiphonia*	36.21	*Polysiphonia*	39.85	*Polysiphonia*	35.76
Polysiphonia	27.18	*Padina*	23.58	*Padina*	29.95	*Sphacelaria*	22.51	*Sphacelaria*	29.91
Padina	14.55	*Sphacelaria*	7.53	*Sphacelaria*	23.33	*Chaetomorpha*	13.28	*Chaetomorpha*	10.61
Chaetomorpha	6.91	*Chaetomorpha*	2.27	*Chaetomorpha*	3.57	*Padina*	12.17	*Enteromorpha*	6.41
Enteromorpha	4.60	*Centroceras*	0.94	*Hypnea*	2.04	*Enteromorpha*	3.01	*Padina*	6.04
Microalgae	3.45	*Bryopsis*	0.87	Phaeophyte (juv.)	1.15	*Cladophora*	2.92	*Centroceras*	2.36
Feldmannia/Hincksia	2.46	*Enteromorpha*	0.75	*Bryopsis*	1.02	*?Ulvella*	1.81	*Hormophysa*	2.22
Cladophora	2.40	*Crouania*	0.50	*Enteromorpha*	0.97	*Fosliella*	1.60	Phaeophyte (juv.)	2.04
Centroceras	1.15	Phaeophyte (juv.)	0.44	*?Ulvella*	0.51	*Crouania*	1.40	*Cladophora*	1.00
Phaeophyte (juv.)	0.83	*Ceramium*	0.41	*Fosliella*	0.31	*Hypnea*	0.46	Microalgae	0.83
Herposiphonia	0.72	*Cladophora*	0.32	*Crouania*	0.27	*Centroceras*	0.32	*Ceramium*	0.65
?Ulvella	0.72	*Spyridia*	0.17	*Centroceras*	0.23	*Feldmannia/Hincksia*	0.30	*Feldmannia/Hincksia*	0.62
Bryopsis	0.38	Microalgae	0.14	*Feldmannia/Hincksia*	0.19	*Bryopsis*	0.27	*Crouania*	0.43
Ceramium	0.32	*?Ulvella*	0.12	*Spyridia*	0.08	*Ceramium*	0.05	*Spyridia*	0.32
Fosliella	0.24	*Fosliella*	0.05	Microalgae	0.05	Phaeophyte (juv.)	0.03	*?Ulvella*	0.28
Crouania	0.13	*Hormophysa*	0.04	*Jania*	0.04	Microalgae	0.02	*Hypnea*	0.19
Gelidium	0.06	*Feldmannia/Hincksia*	0.03	*Herposiphonia*	0.04			*Bryopsis*	0.15
		Hypnea	0.02	*Ceramium*	0.03			*Fosliella*	0.06
				Chondria	0.03			*Cladophora*	0.05
				Cladophora	0.01			*Anotrichium*	0.05
								Gelidium	0.03

Table 6.6: **Ranked abundance** of all genera recorded in the algal communities growing in all treatments at Abu Ali from June 1994 until July 1994. The genera are listed in decreasing order of abundance based on their total volumetric cover multiplied by the number of times each genus was recorded during the 12-month study period. This relative dominance is given as a percentage of the total abundance of the community.

Treatment 1		Treatment 2		Treatment 3		Treatments 5 & 6	
Genera	**%**	**Genera**	**%**	**Genera**	**%**	**Genera**	**%**
?Ulvella	35.62	*Hypnea*	48.69	Microalgae	35.04	Microalgae	33.64
Microalgae	30.98	*Polysiphonia*	31.05	*?Ulvella*	27.53	*Feldmannia/Hincksia*	28.55
Feldmannia/Hincksia	25.19	*Sphacelaria*	8.21	*Sphacelaria*	16.45	*?Ulvella*	19.03
Sphacelaria	4.86	Microalgae	4.95	*Feldmannia/Hincksia*	14.66	*Acrochaetium*	10.00
Acrochaetium	1.27	*Lobophora*	2.13	*Polysiphonia*	1.97	*Sphacelaria*	3.36
Cladophora	0.80	*Ceramium*	1.76	*Fosliella*	1.43	*Herposiphonia*	2.44
Polysiphonia	0.75	*?Ulvella*	1.05	*Acrochaetium*	1.07	*?Peyssonnelia*	1.15
Herposiphonia	0.25	*Feldmannia/Hincksia*	0.99	*?Peyssonnelia*	0.60	*Polysiphonia*	1.06
Ceramium	0.15	*Anotrichium*	0.47	*Ceramium*	0.48	*Fosliella*	0.32
Anotrichium	0.05	*Herposiphonia*	0.28	*Herposiphonia*	0.36	*Anotrichium*	0.19
Fosliella	0.05	*Cladophora*	0.15	*Lobophora*	0.18	*Enteromorpha*	0.13
?Peyssonnelia	0.03	*Acrochaetium*	0.13	*Enteromorpha*	0.12	*Ceramium*	0.06
		Aglaothamnion	0.05	*Anotrichium*	0.06	*Bryopsis*	0.03
		Chaetomorpha	0.04	*Centroceras*	0.06	*Gelidium*	0.03
		Gelidium	0.04				
		Fosliella	0.03				
		Bryopsis	0.01				

Table 6.7: **Ranked abundance** of all genera recorded in the algal communities growing in all treatments at Jana (shallow) from June 1994 until April 1995. The genera are listed in decreasing order of abundance based on their total volumetric cover multiplied by the number of times each genus was recorded during the sampling period. This relative dominance is given as a percentage of the total abundance of the community.

Treatment 1		Treatment 2		Treatment 3		Treatment 4		Treatments 5 & 6	
Genera	**%**	**Genera**	**%**	**Genera**	**%**	**Genera**	**%**	**Genera**	**%**
?Peyssonnelia	40.81	*Acrochaetium*	36.13	*?Peyssonnelia*	30.20	Microalgae	24.41	*?Peyssonnelia*	33.84
?Ulvella	23.25	*Sphacelaria*	18.22	Microalgae	17.17	*?Peyssonnelia*	15.60	*?Ulvella*	25.12
Microalgae	15.22	*?Peyssonnelia*	17.15	*?Ulvella*	17.09	*Acrochaetium*	14.56	Microalgae	20.52
Feldmannia/Hincksia	5.22	Microalgae	8.08	*Acrochaetium*	8.80	*?Ulvella*	13.11	*Feldmannia/Hincksia*	10.19
Acrochaetium	4.94	*Feldmannia/Hincksia*	5.92	*Feldmannia/Hincksia*	8.43	*Polysiphonia*	11.63	*Acrochaetium*	3.93
Sphacelaria	3.76	*?Ulvella*	4.05	*Polysiphonia*	7.02	*Feldmannia/Hincksia*	8.00	*Sphacelaria*	3.35
Polysiphonia	2.02	*Cladophora*	3.63	*Sphacelaria*	5.27	*Bryopsis*	4.05	*Fosliella*	1.53
Fosliella	1.94	*Polysiphonia*	3.57	*Bryopsis*	2.81	*Sphacelaria*	2.93	*Cladophora*	0.64
Anotrichium	1.38	*Bryopsis*	1.58	*Anotrichium*	1.17	*Anotrichium*	2.60	*Polysiphonia*	0.49
Bryopsis	0.63	*Aglaothamnion*	0.61	*Fosliella*	1.05	*Fosliella*	1.40	*Bryopsis*	0.22
Cladophora	0.42	*Lobophora*	0.35	*Cladophora*	0.70	*Herposiphonia*	0.77	*Anotrichium*	0.15
Ceramium	0.16	*Hypnea*	0.30	*Aglaothamnion*	0.16	*Cladophora*	0.65	*Aglaothamnion*	0.04
Aglaothamnion	0.08	*Anotrichium*	0.25	*Herposiphonia*	0.12	*Ceramium*	0.14	*Herposiphonia*	0.02
		Crouania	0.08	*Enteromorpha*	0.02	*Aglaothamnion*	0.14		
		Fosliella	0.05						
		Trichosolen	0.03						

Table 6.8: **Ranked abundance** of all genera recorded in the algal communities growing in all treatments at Jana (deep) from June 1994 until April 1995. The genera are listed in decreasing order of abundance based on their total volumetric cover multiplied by the number of times each genus was recorded during the 12-month study period. This relative dominance is given as a percentage of the total abundance of the community.

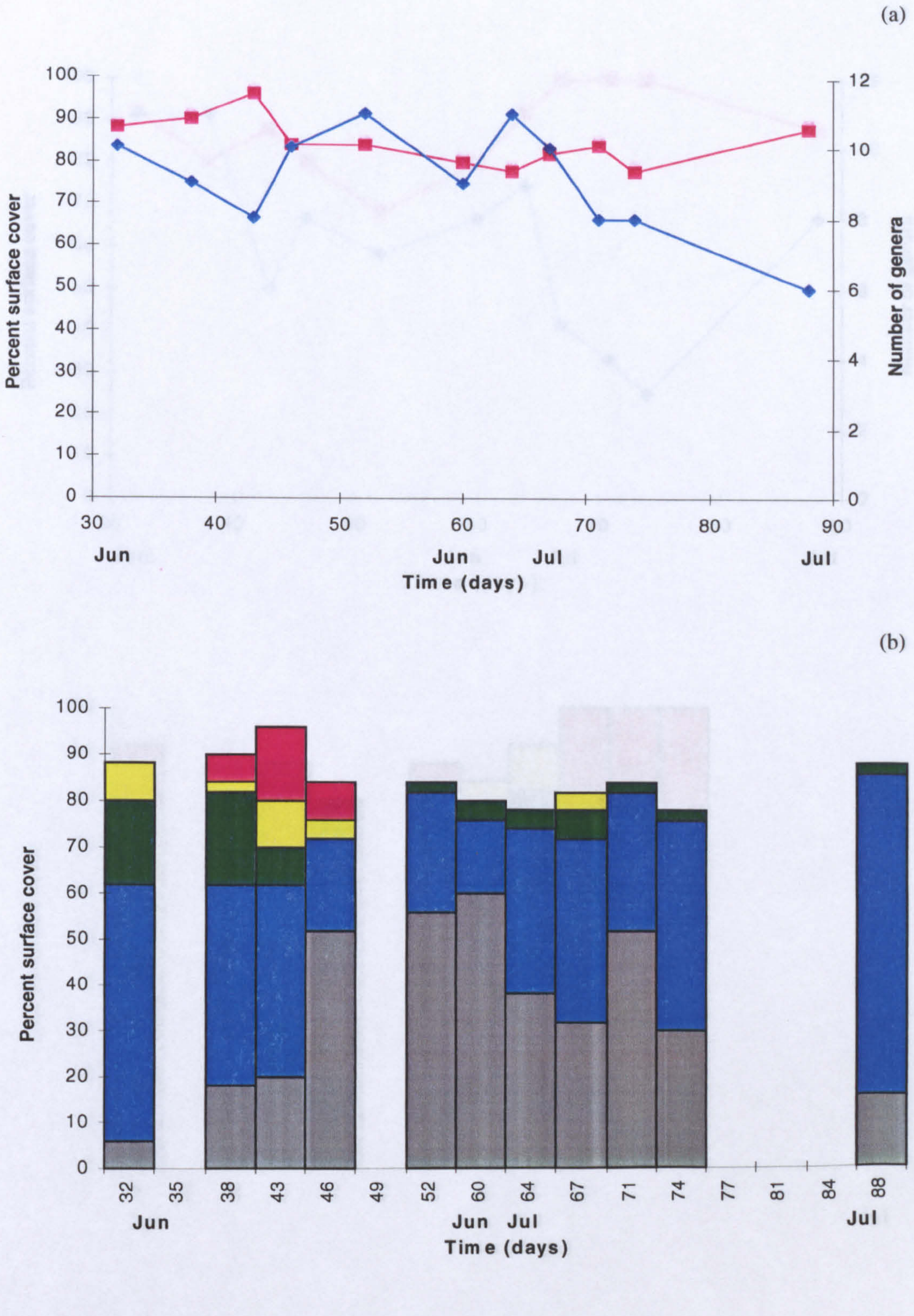
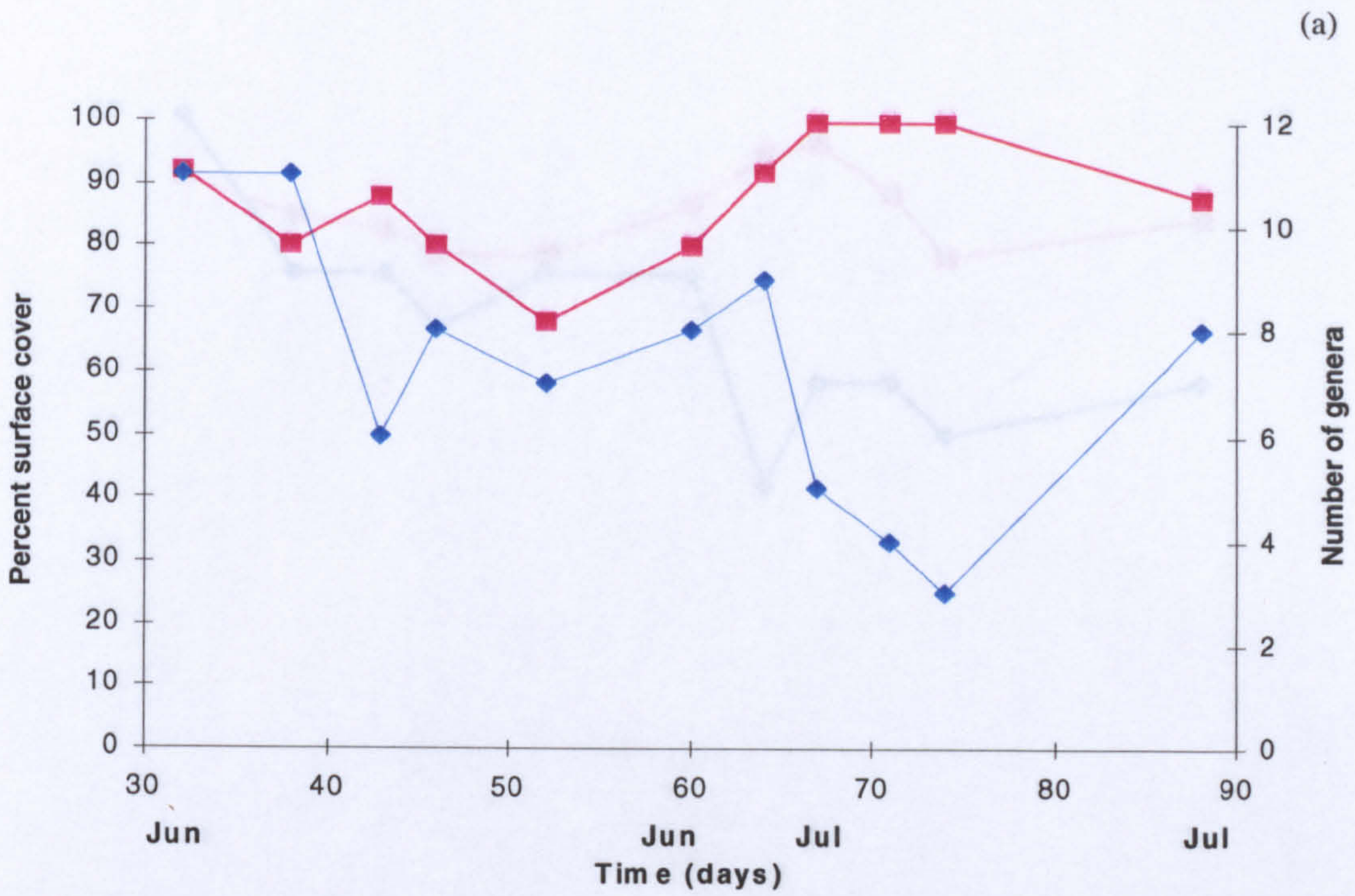


Figure 6.1: Composition and structure of the algal community on **Treatment 1** at **Abu Ali**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).



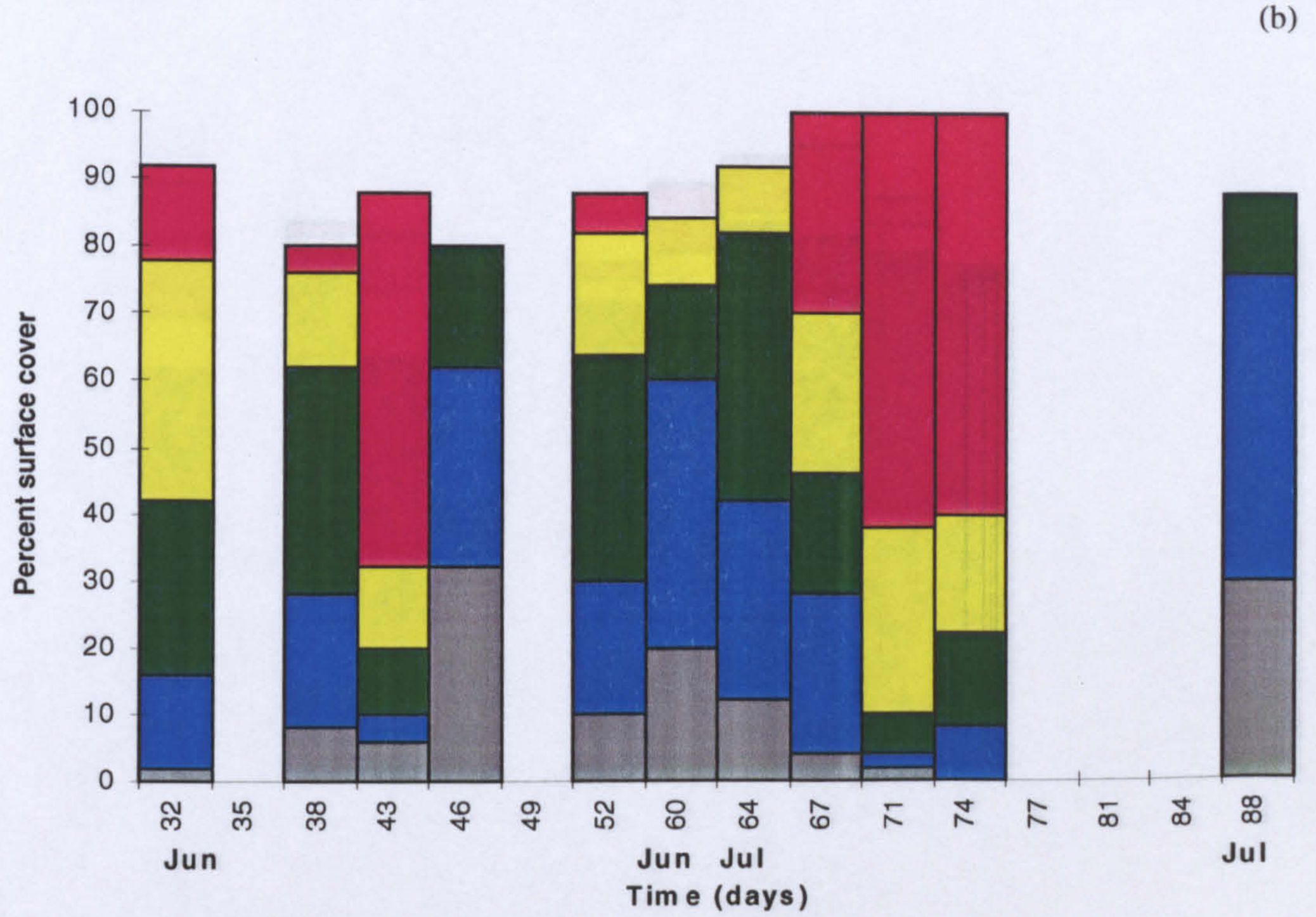


Figure 6.2: Composition and structure of the algal community on **Treatment 2** at **Abu Ali**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).

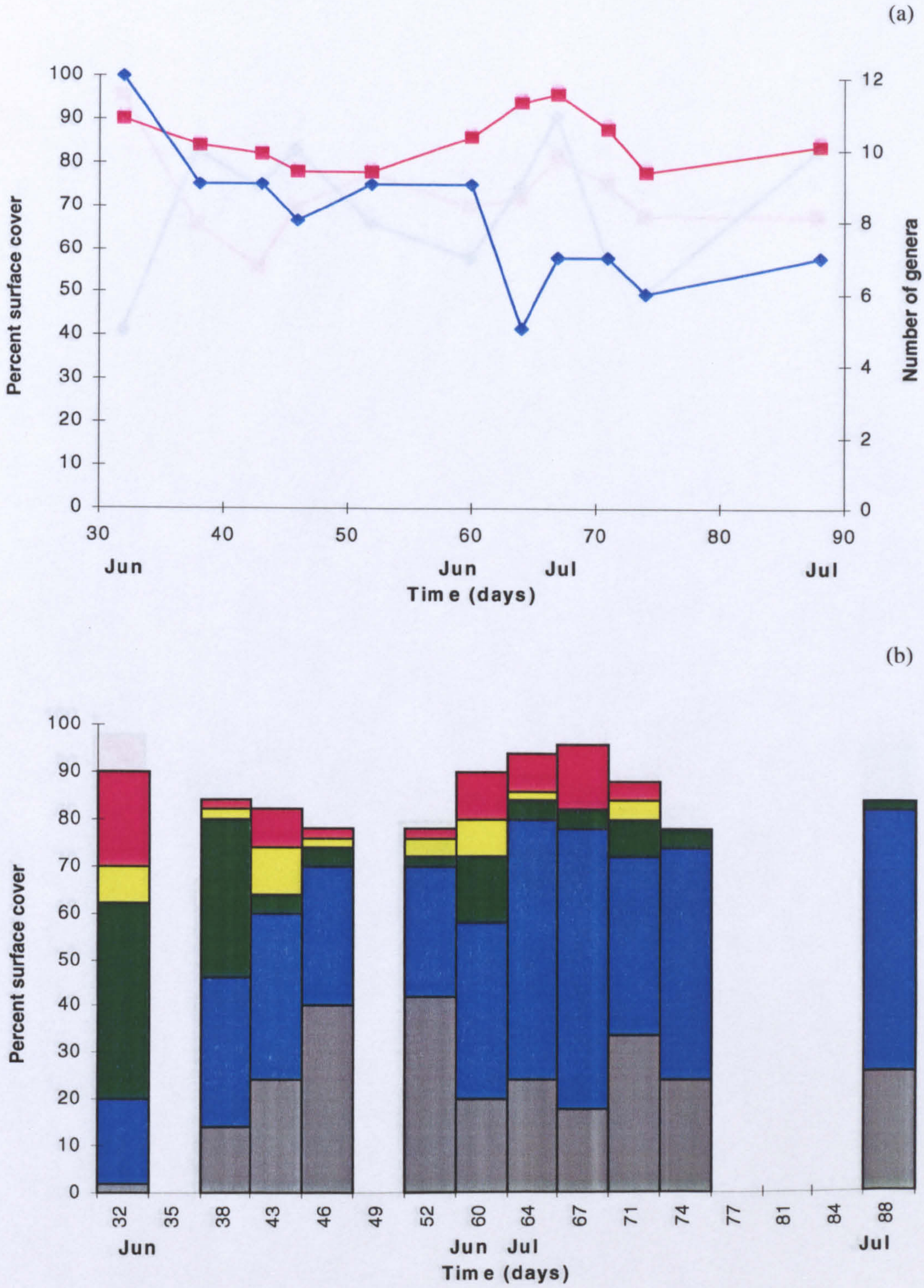
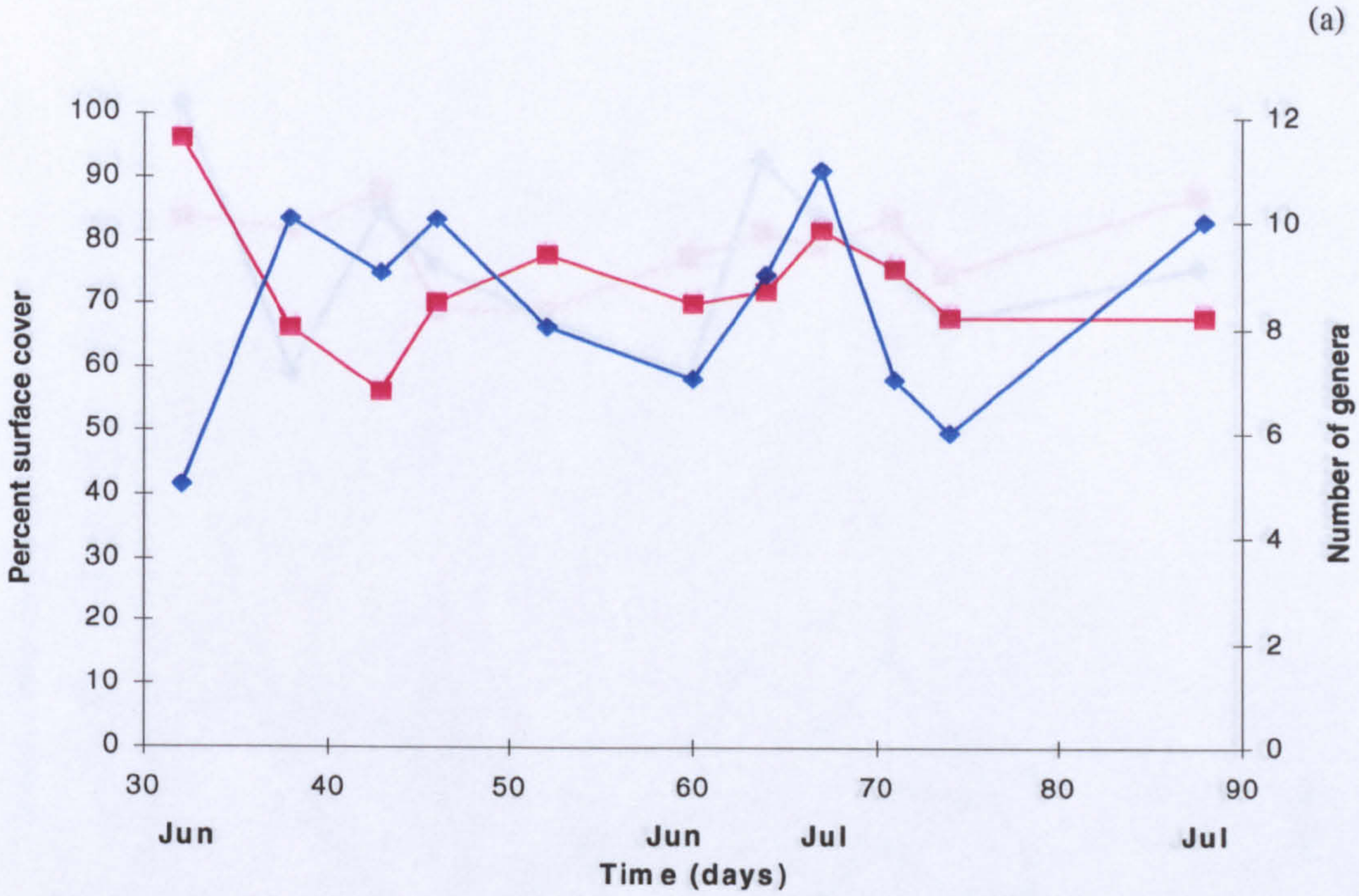


Figure 6.3: Composition and structure of the algal community on **Treatment 3** at **Abu Ali**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).



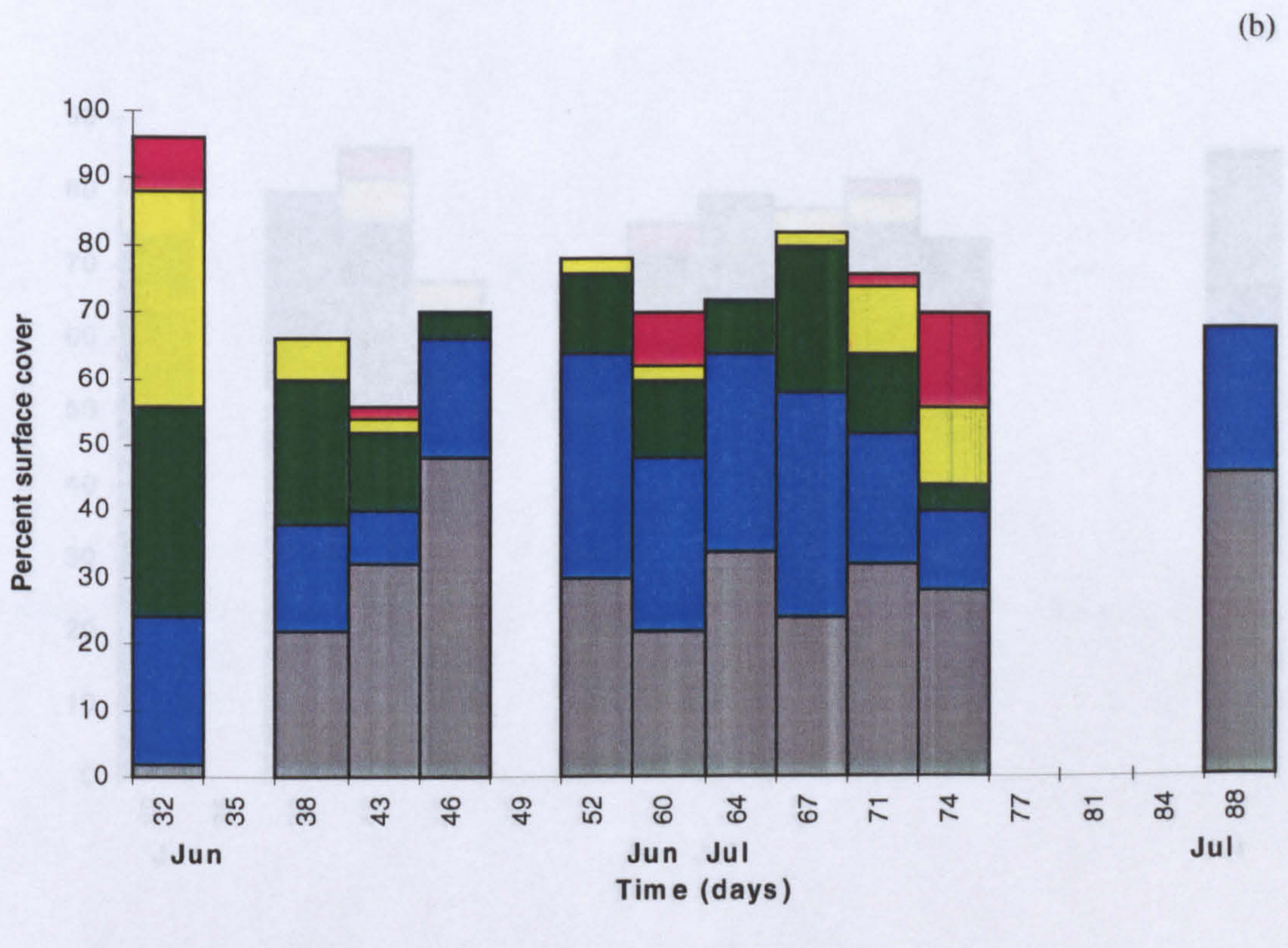


Figure 6.4: Composition and structure of the algal community on **Treatment 4** at **Abu Ali**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).

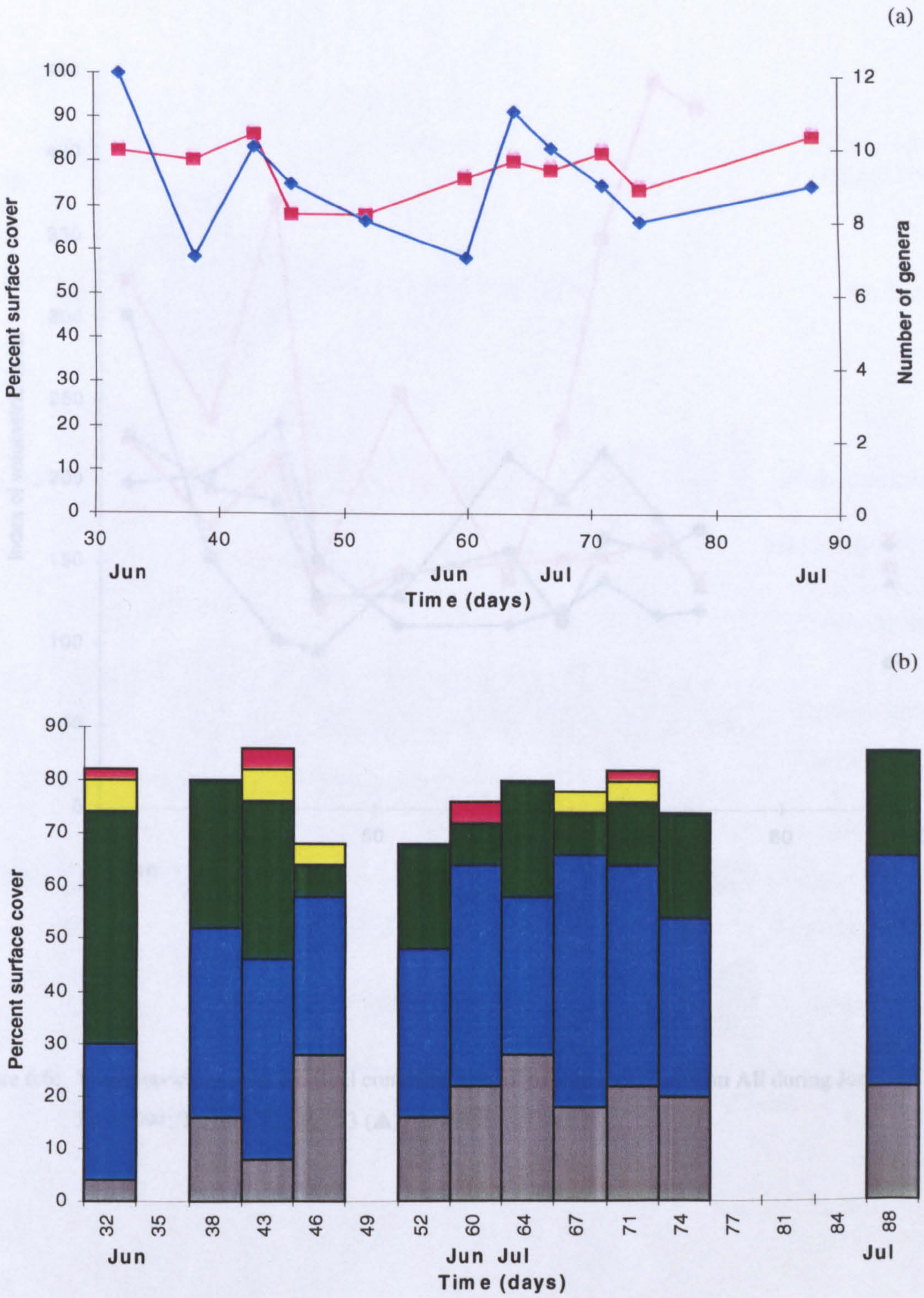


Figure 6.5: Composition and structure of the algal community on **Treatments 5 & 6** (pooled) at **Abu Ali**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).

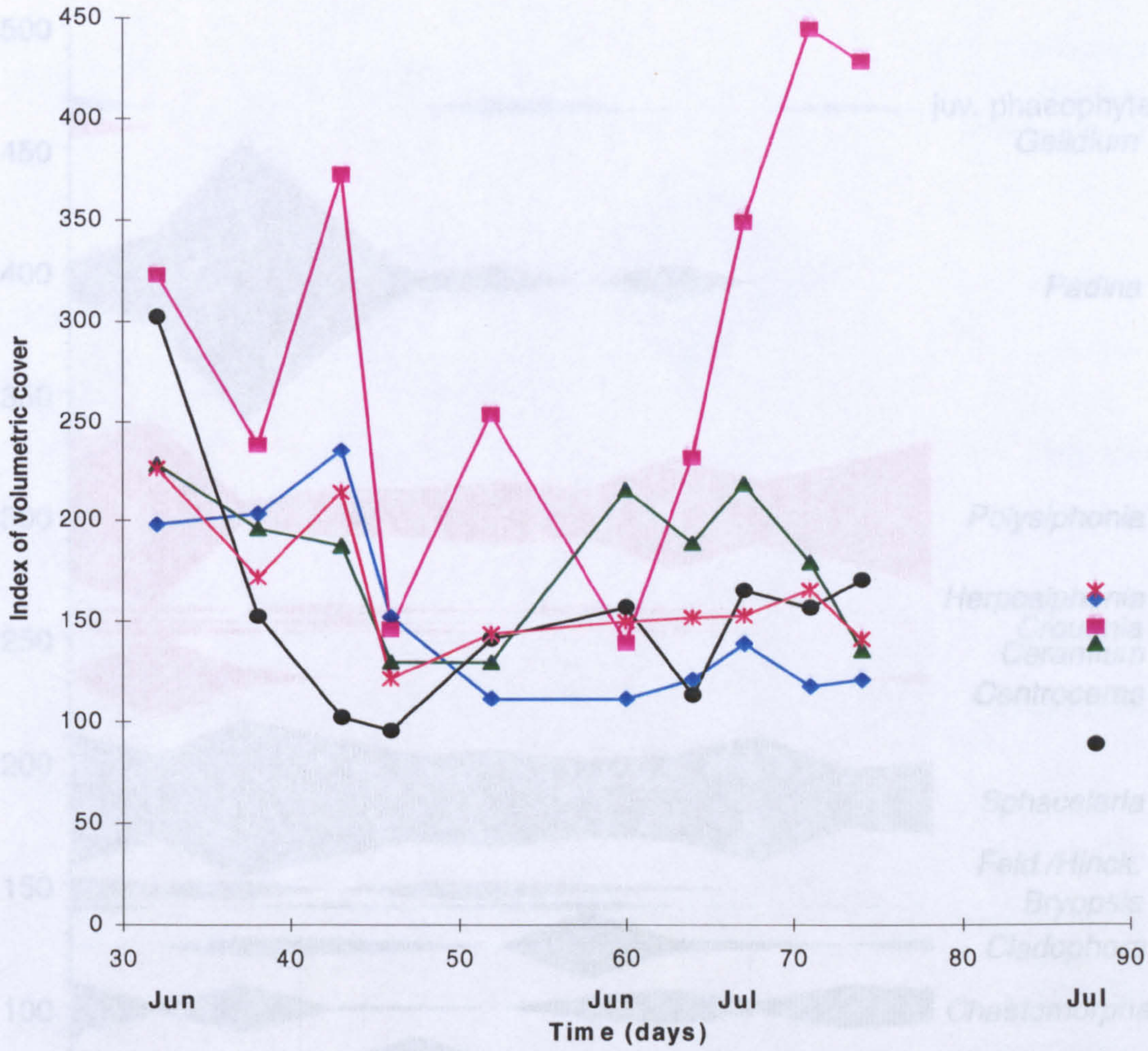


Figure 6.6: **Volumetric cover** of the algal community on all treatments (T) at **Abu Ali** during June and July 1994; T1 (◆), T2 (■), T3 (▲), T4 (●) and T5&6 (✳).

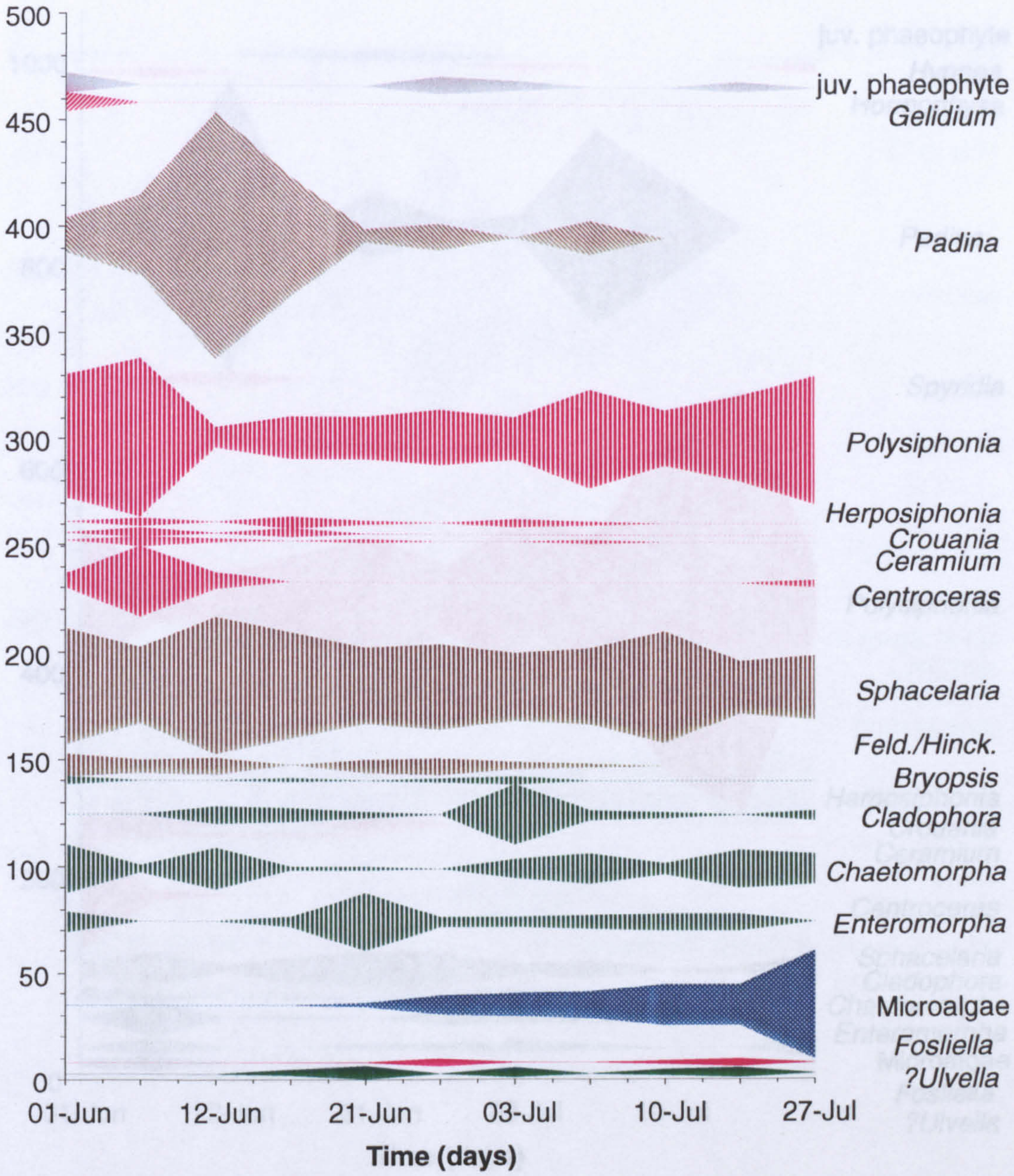


Figure 6.7: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 1** at **Abu Ali** during June and July 1994.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

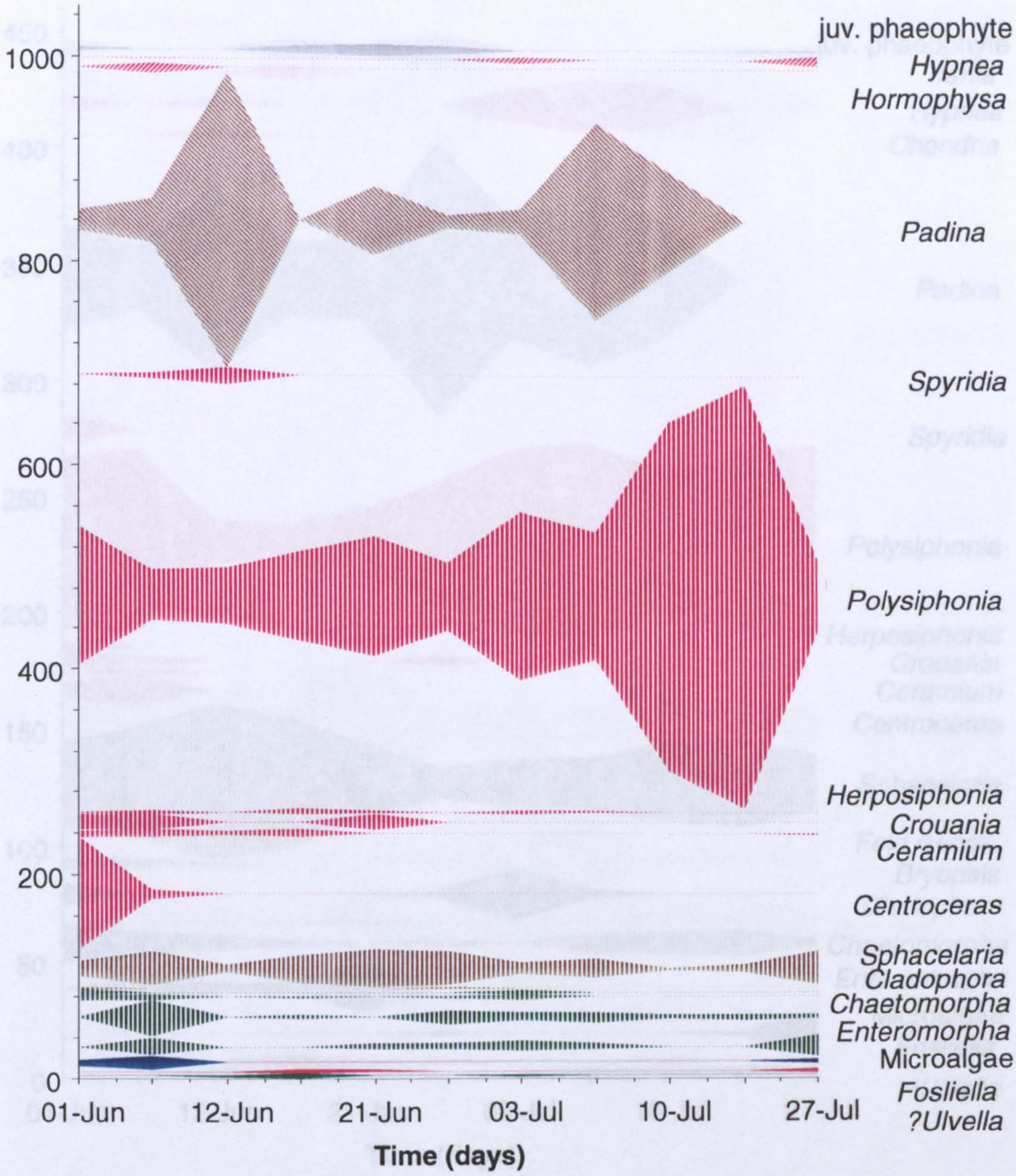


Figure 6.8: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 2** at **Abu Ali** during June and July 1994.

crustose	microalgae	filamentous
corticated-foliose	corticated macrophytes	articulated calcareous
Chlorophyta	Phaeophyta	Rhodophyta

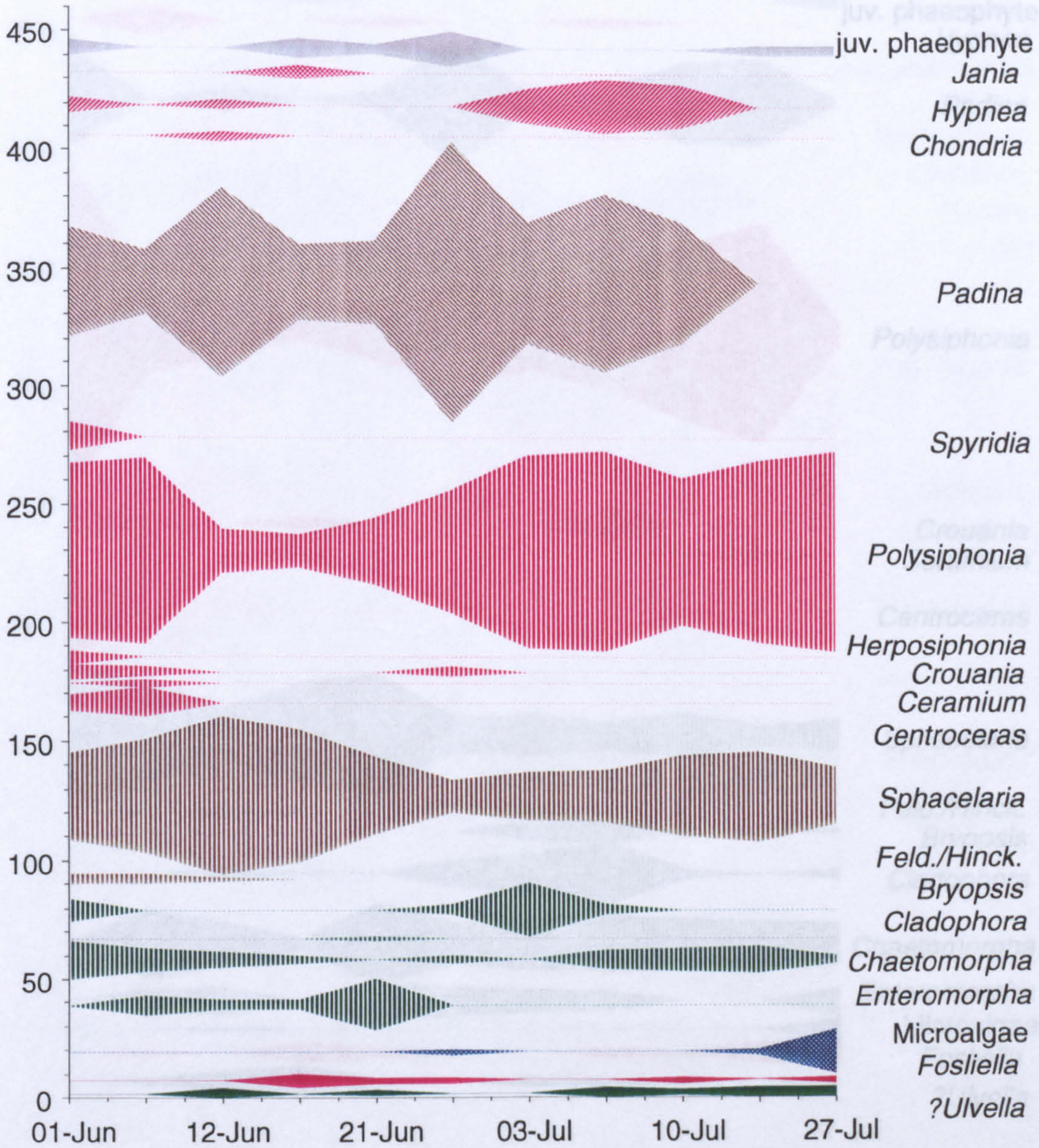


Figure 6.9: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 3** at **Abu Ali** during June and July 1994.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

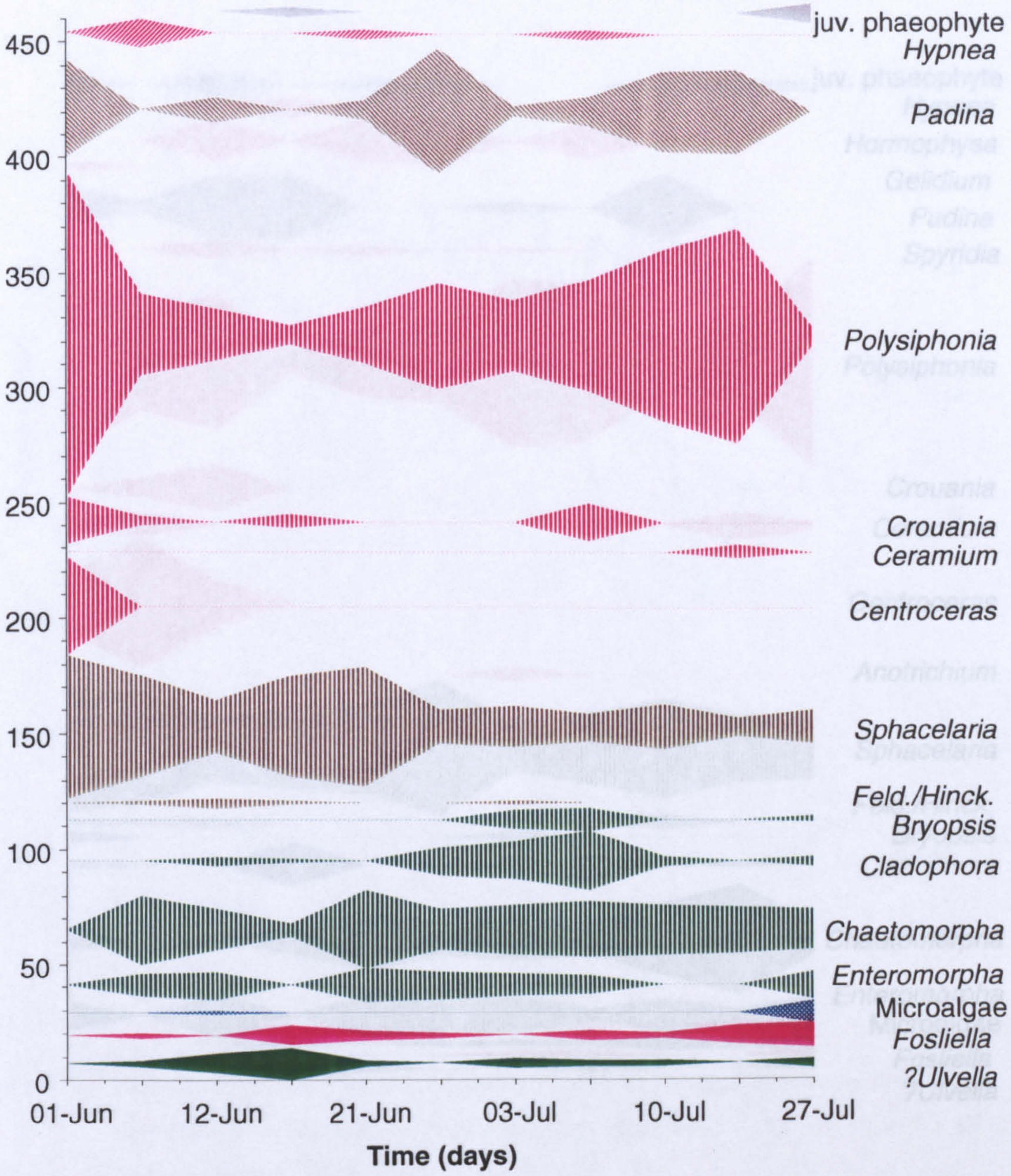


Figure 6.10: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 4** at **Abu Ali** during June and July 1994.

crustose	microalgae	filamentous
corticated-foliose	corticated macrophytes	articulated calcareous
Chlorophyta	Phaeophyta	Rhodophyta

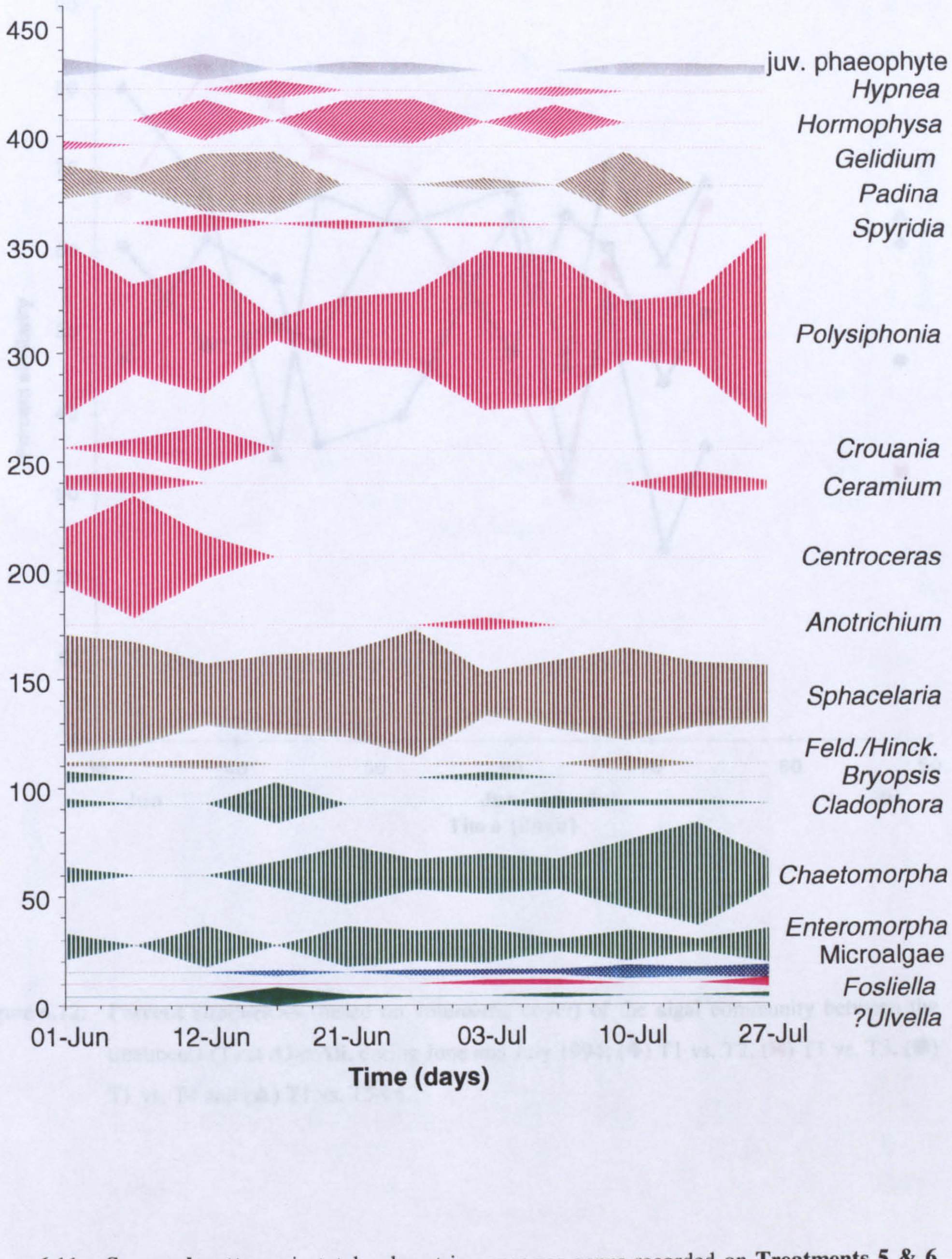


Figure 6.11: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatments 5 & 6** (pooled) at **Abu Ali** during June and July 1994.

crustose	microalgae	filamentous
corticated-foliose	corticated macrophytes	articulated calcareous
Chlorophyta	Phaeophyta	Rhodophyta

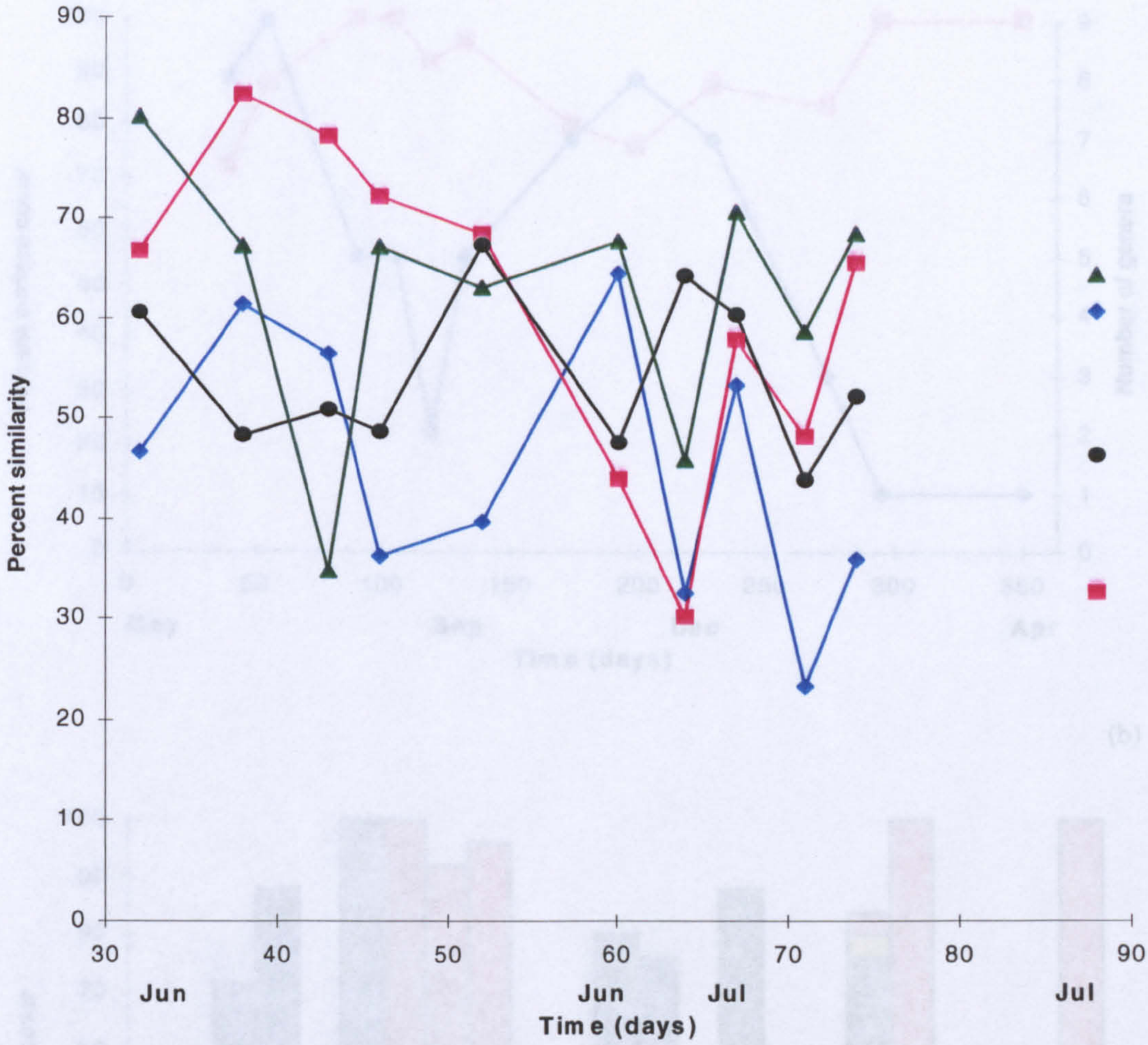
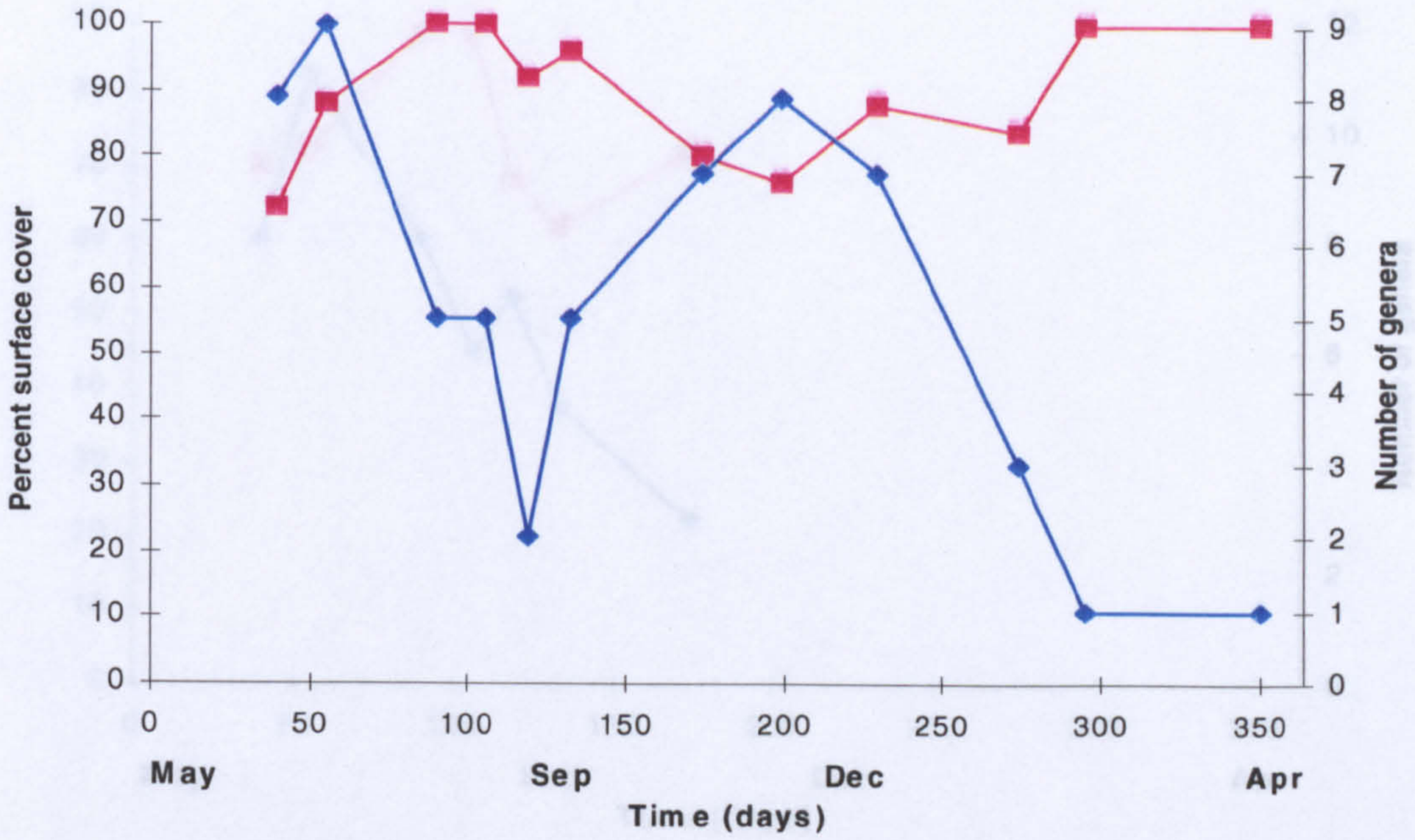


Figure 6.12: **Percent similarities** (based on volumetric cover) of the algal community between the treatments (T) at **Abu Ali**, during June and July 1994; (◆) T1 vs. T2, (■) T1 vs. T3, (●) T1 vs. T4 and (▲) T1 vs. T5&6.

(a)



(b)

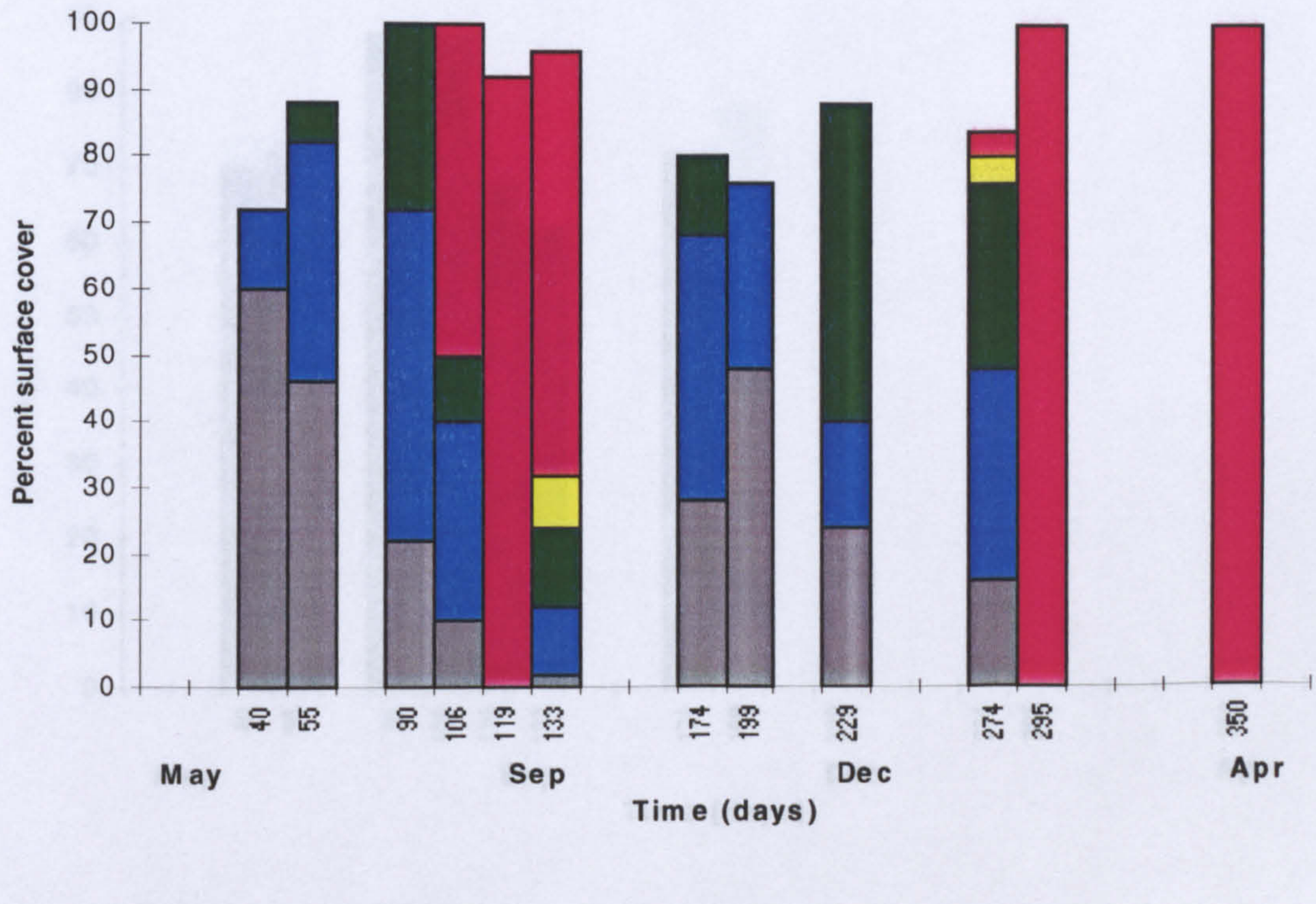


Figure 6.13: Composition and structure of the algal community on **Treatment 2** at **Jana (shallow)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).

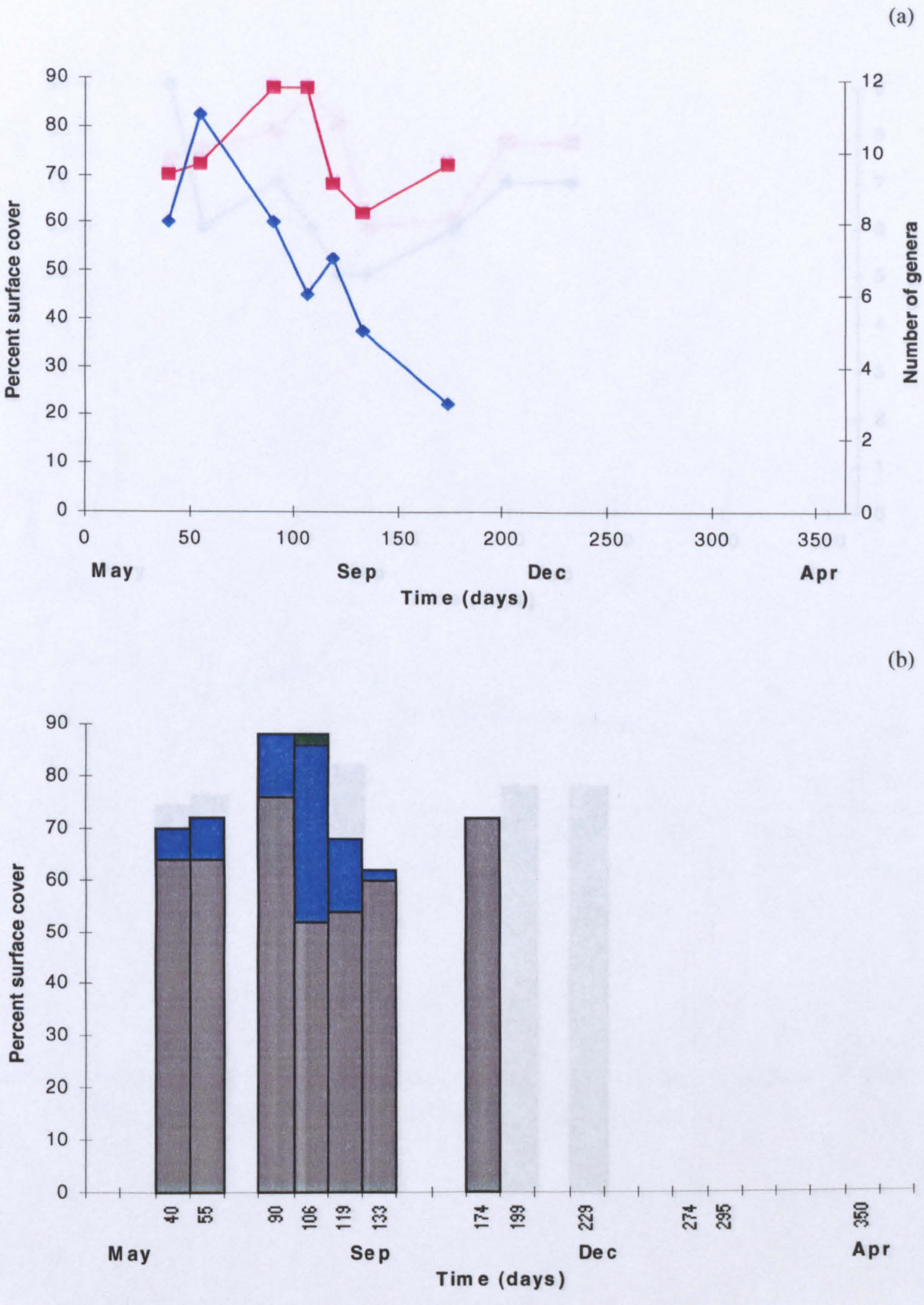


Figure 6.14: Composition and structure of the algal community on **Treatment 3** at **Jana (shallow)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■).

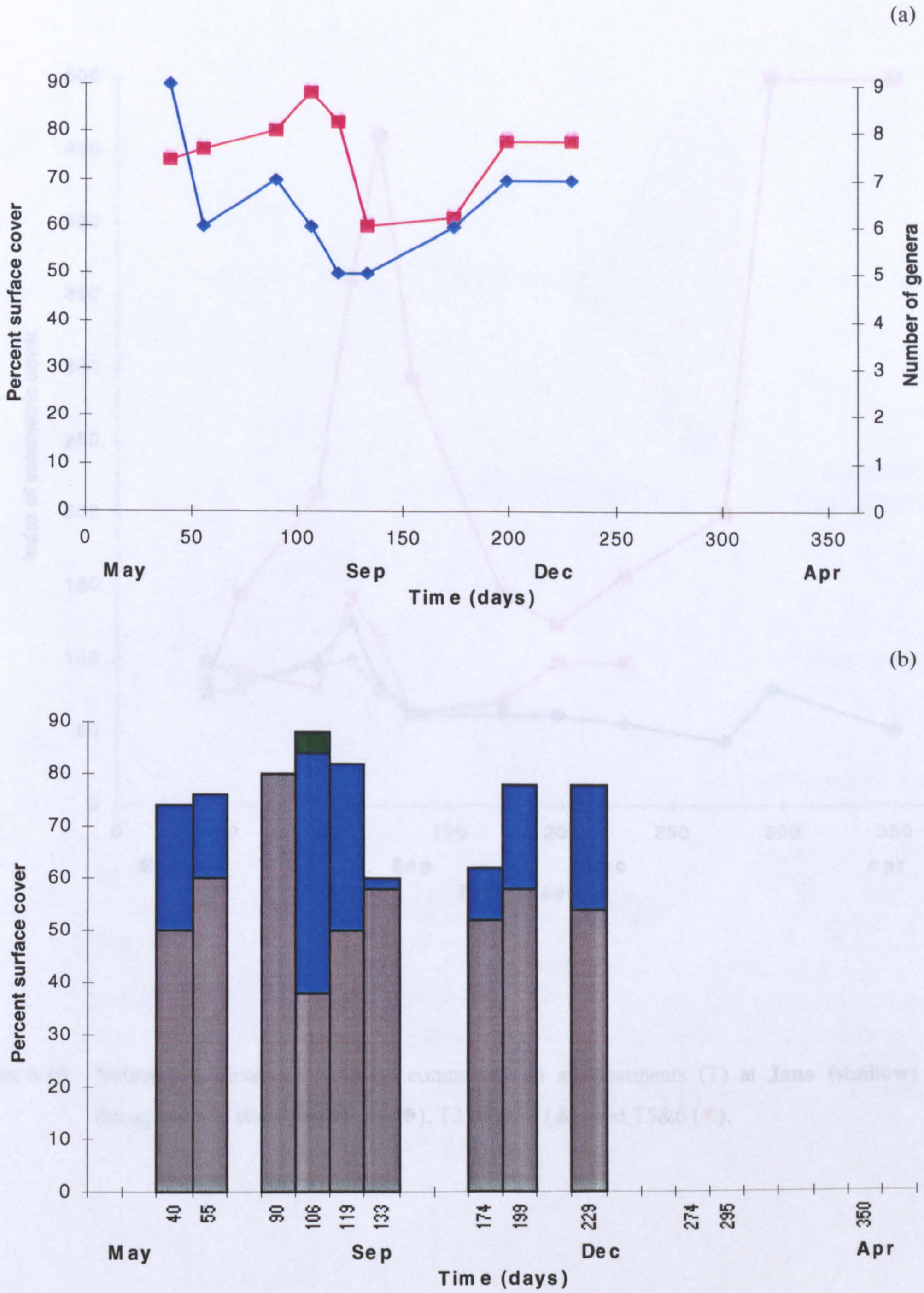


Figure 6.15: Composition and structure of the algal community on **Treatments 5 & 6** (pooled) at **Jana (shallow)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■).

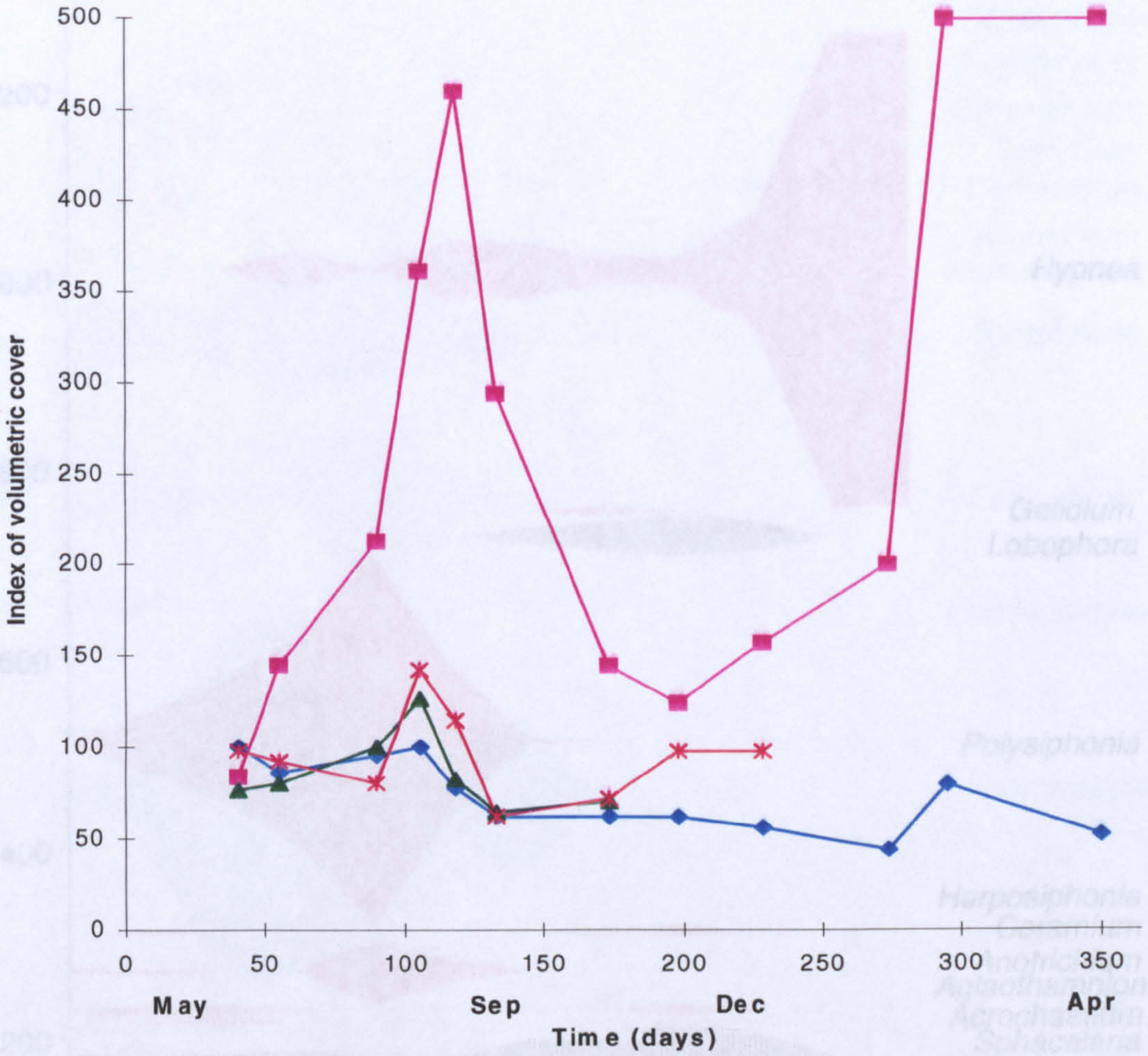


Figure 6.16: **Volumetric cover** of the algal community on all treatments (T) at **Jana (shallow)** throughout the study period; T1 (◆), T2 (■), T3 (▲), and T5&6 (✳).

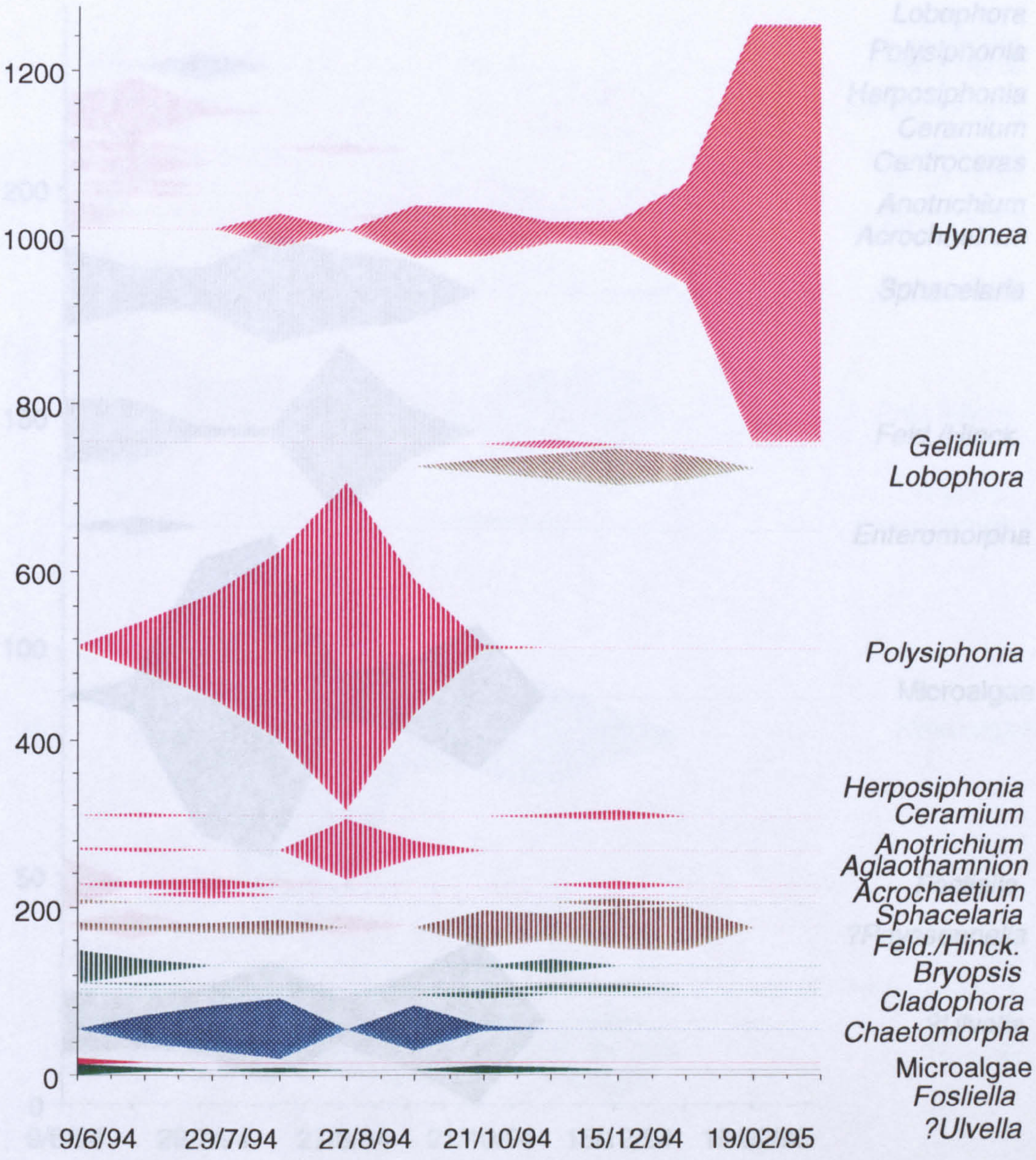


Figure 6.17: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 2** at **Jana (shallow)** throughout the study period.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

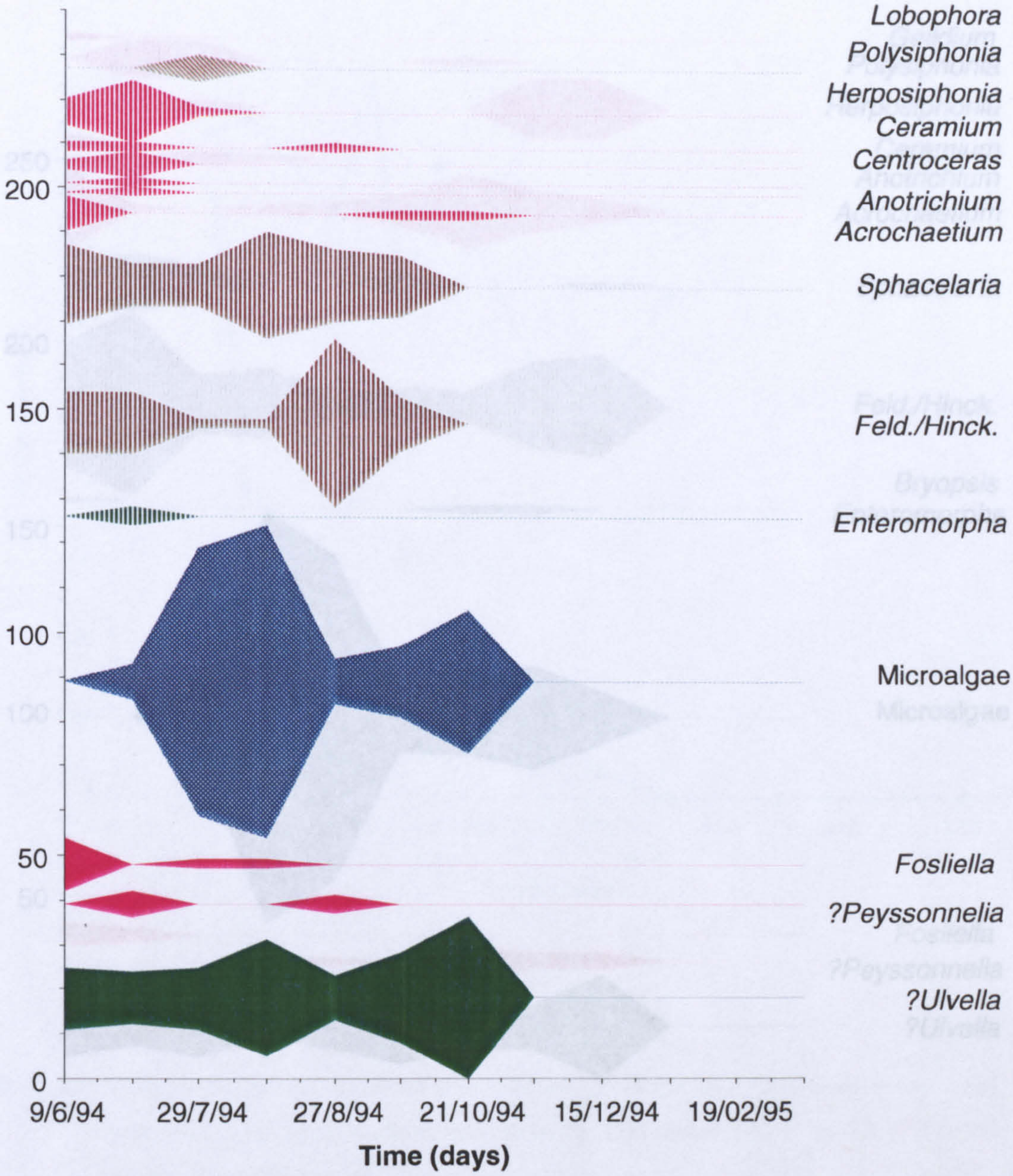


Figure 6.18: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 3** at **Jana (shallow)** throughout the study period.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

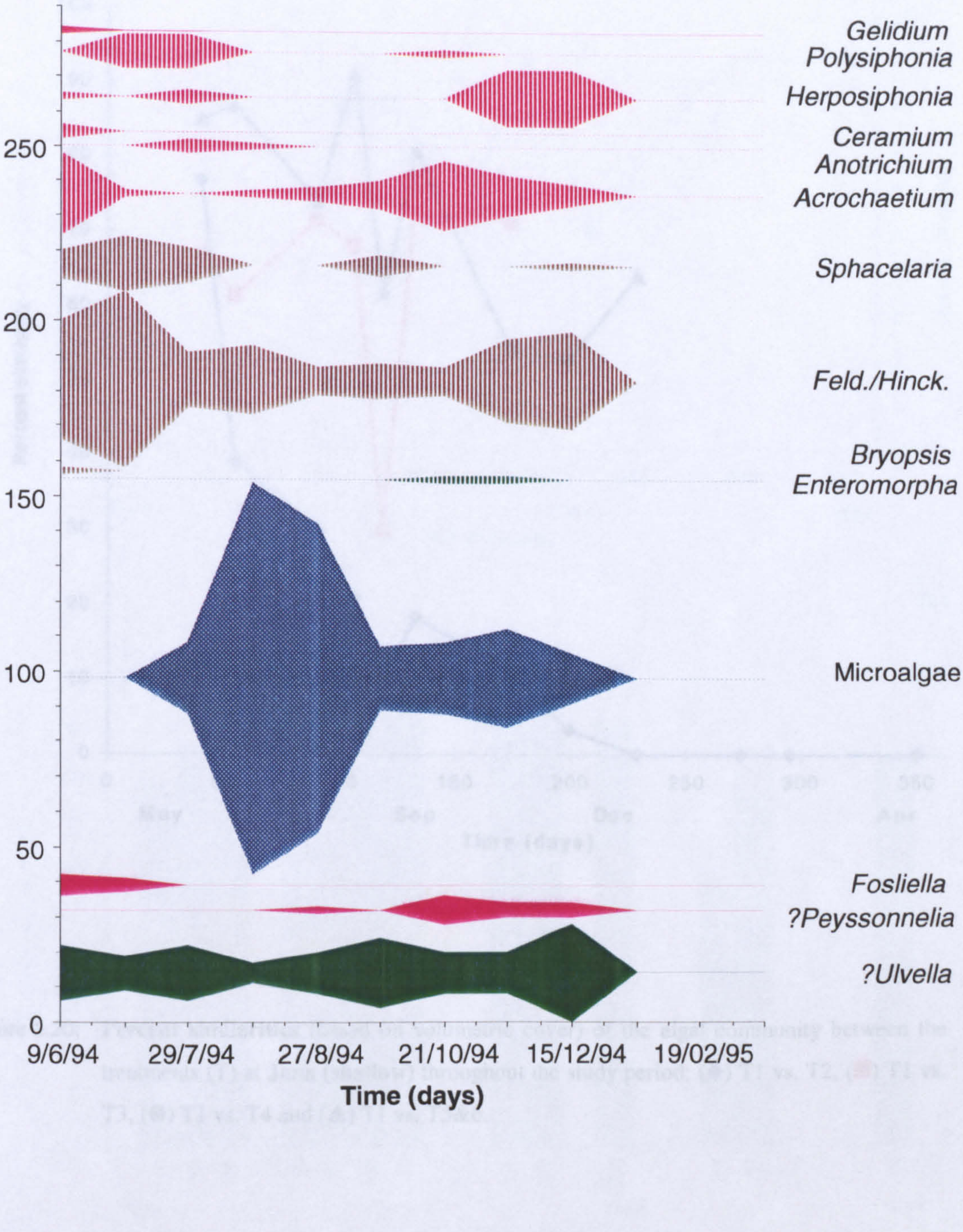


Figure 6.19: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatments 5 & 6** (pooled) at **Jana (shallow)** throughout the study period.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

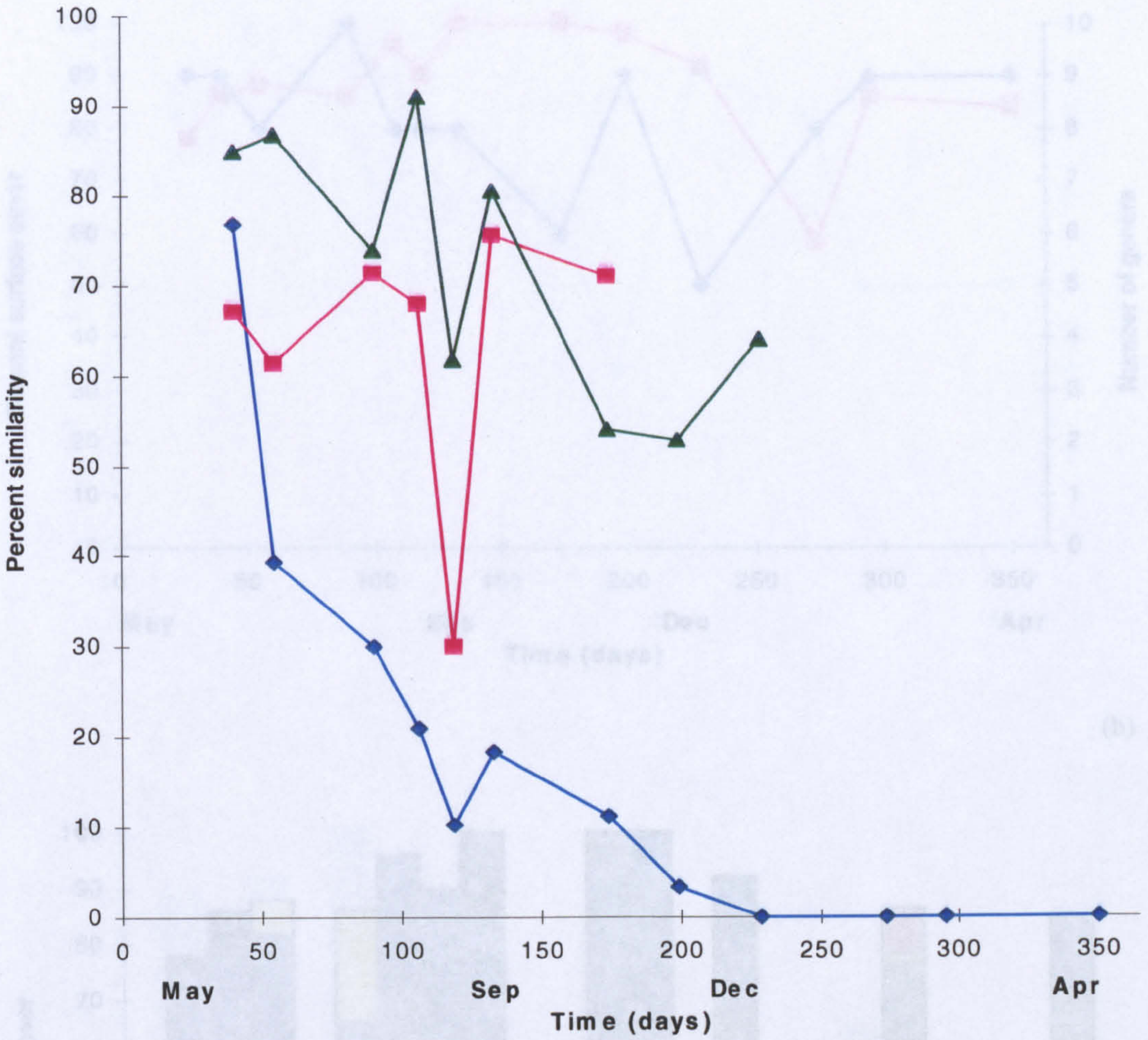
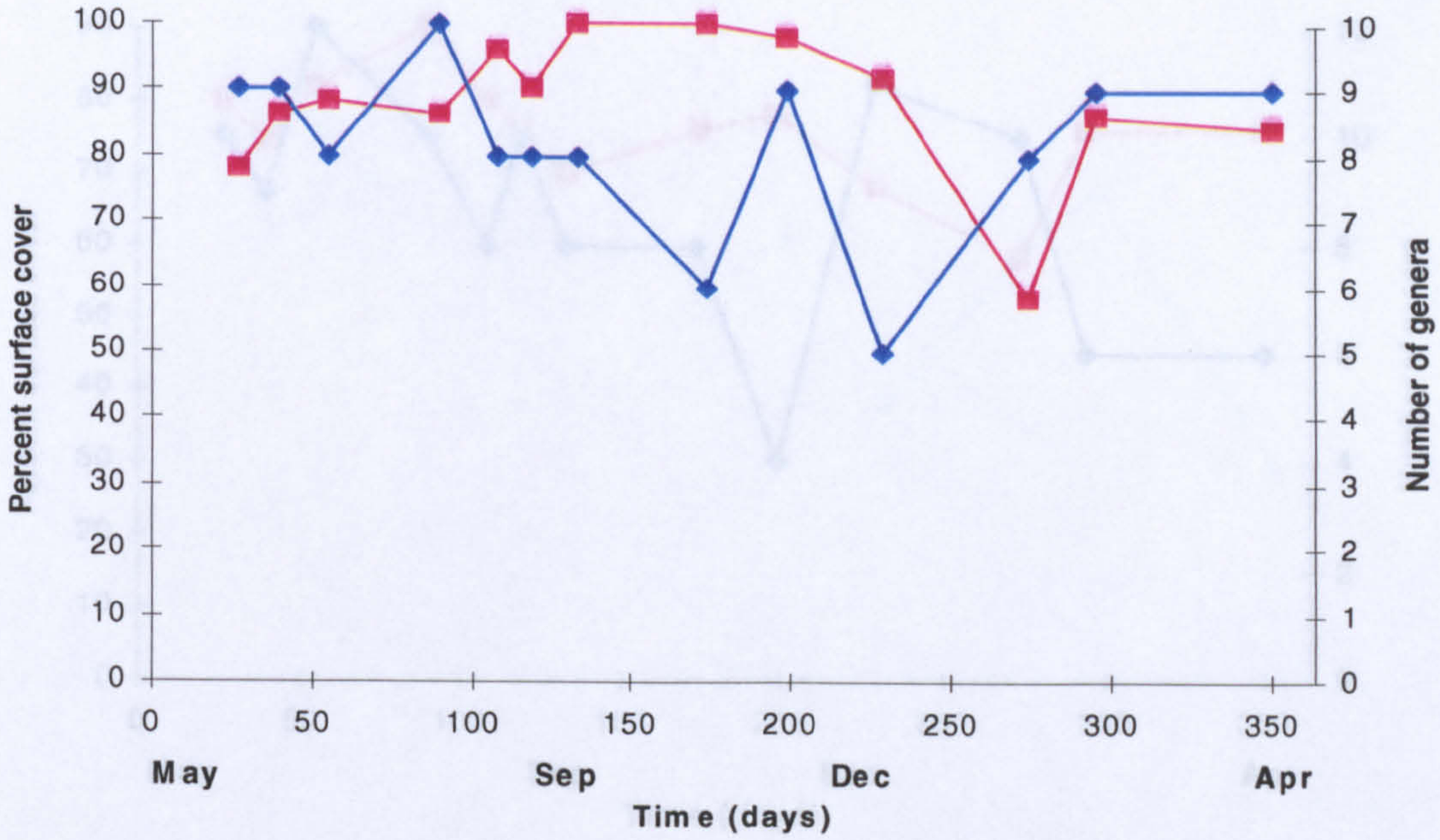


Figure 6.20: **Percent similarities** (based on volumetric cover) of the algal community between the treatments (T) at **Jana (shallow)** throughout the study period; (◆) T1 vs. T2, (■) T1 vs. T3, (●) T1 vs. T4 and (▲) T1 vs. T5&6.

(a)



(b)

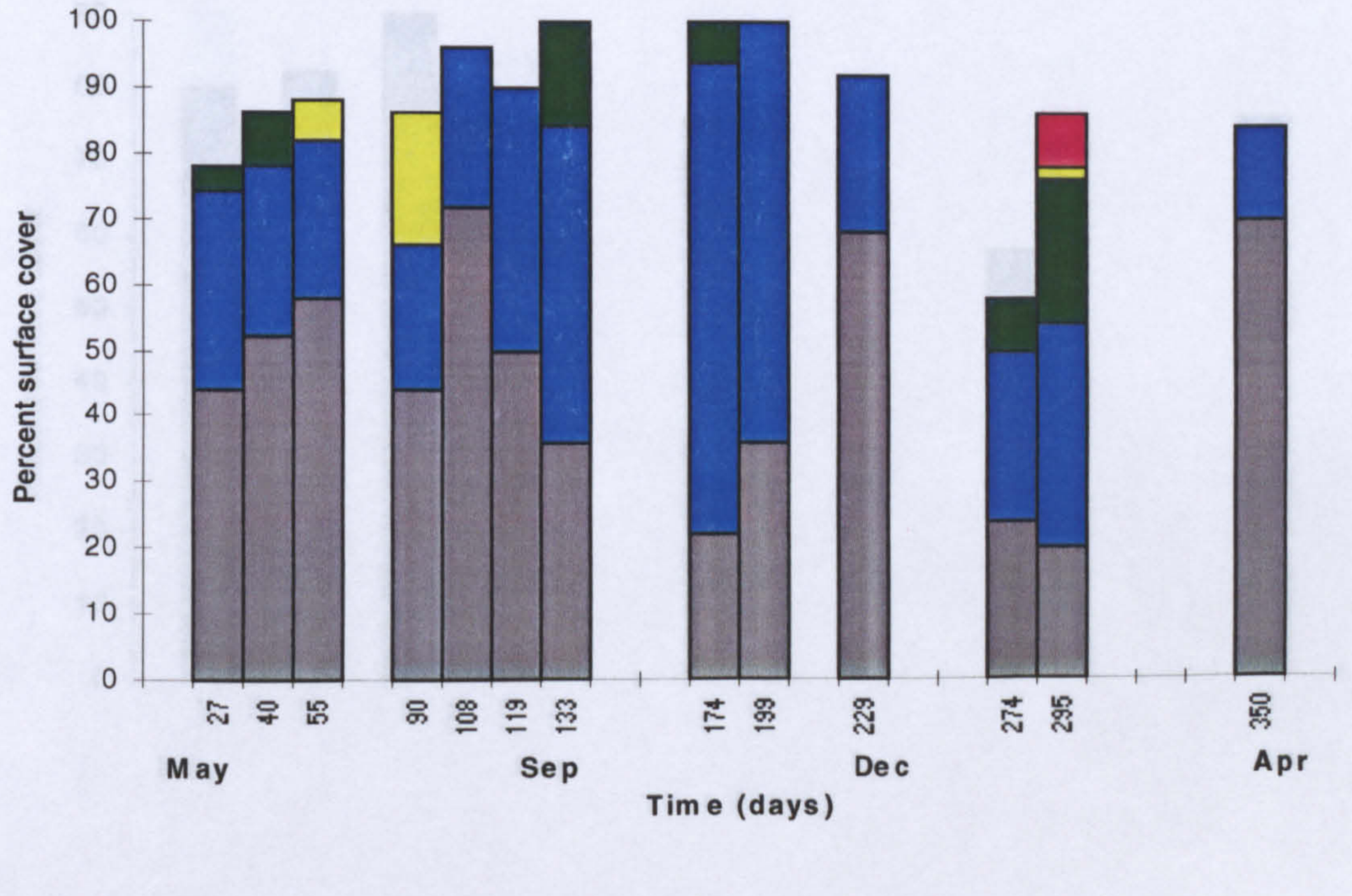


Figure 6.21: Composition and structure of the algal community on **Treatment 2** at **Jana (deep)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■),SC 4 (■), SC 5 (■).

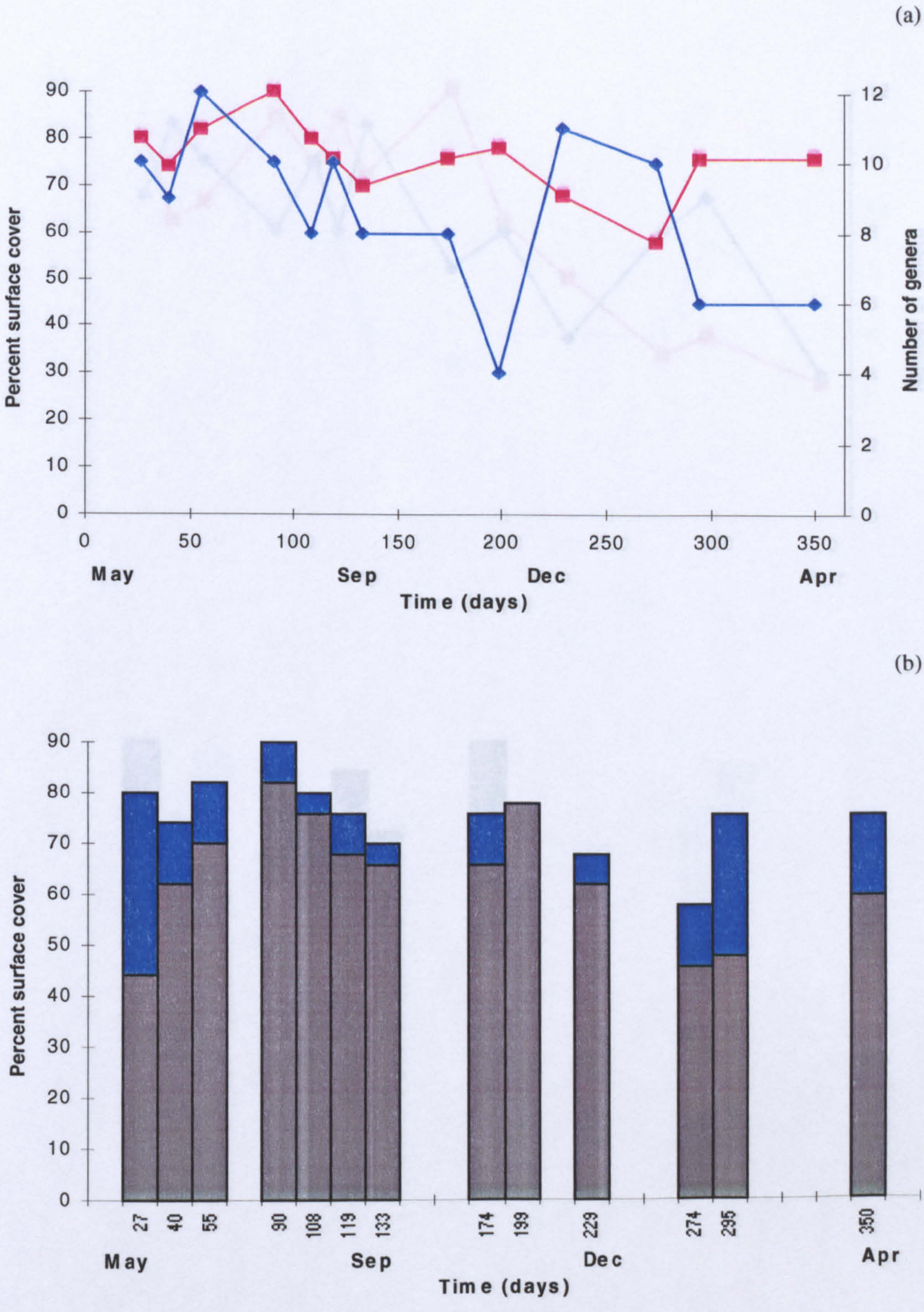


Figure 6.22: Composition and structure of the algal community on **Treatment 3** at **Jana (deep)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■).

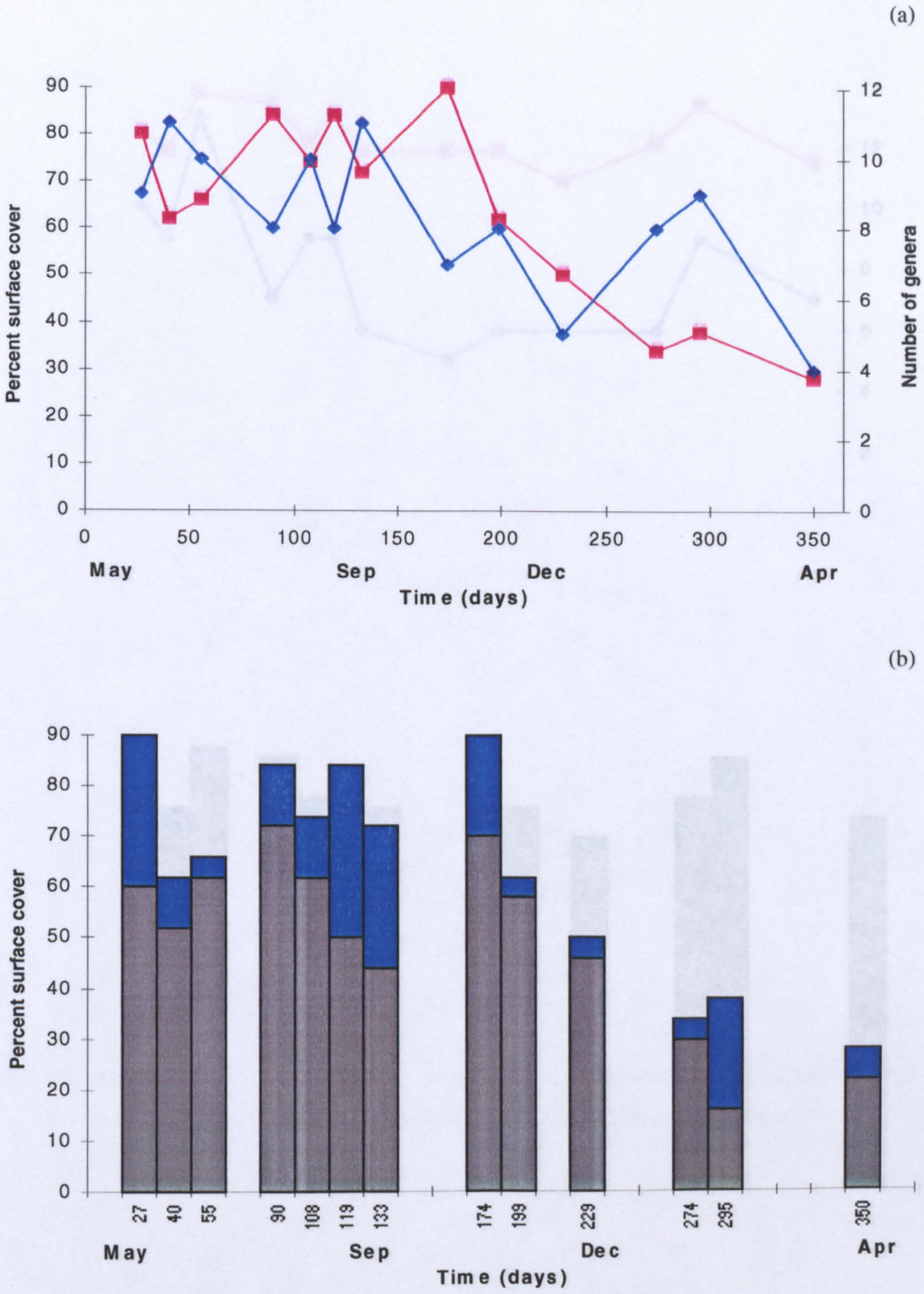


Figure 6.23: Composition and structure of the algal community on **Treatment 4** at **Jana (deep)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■).

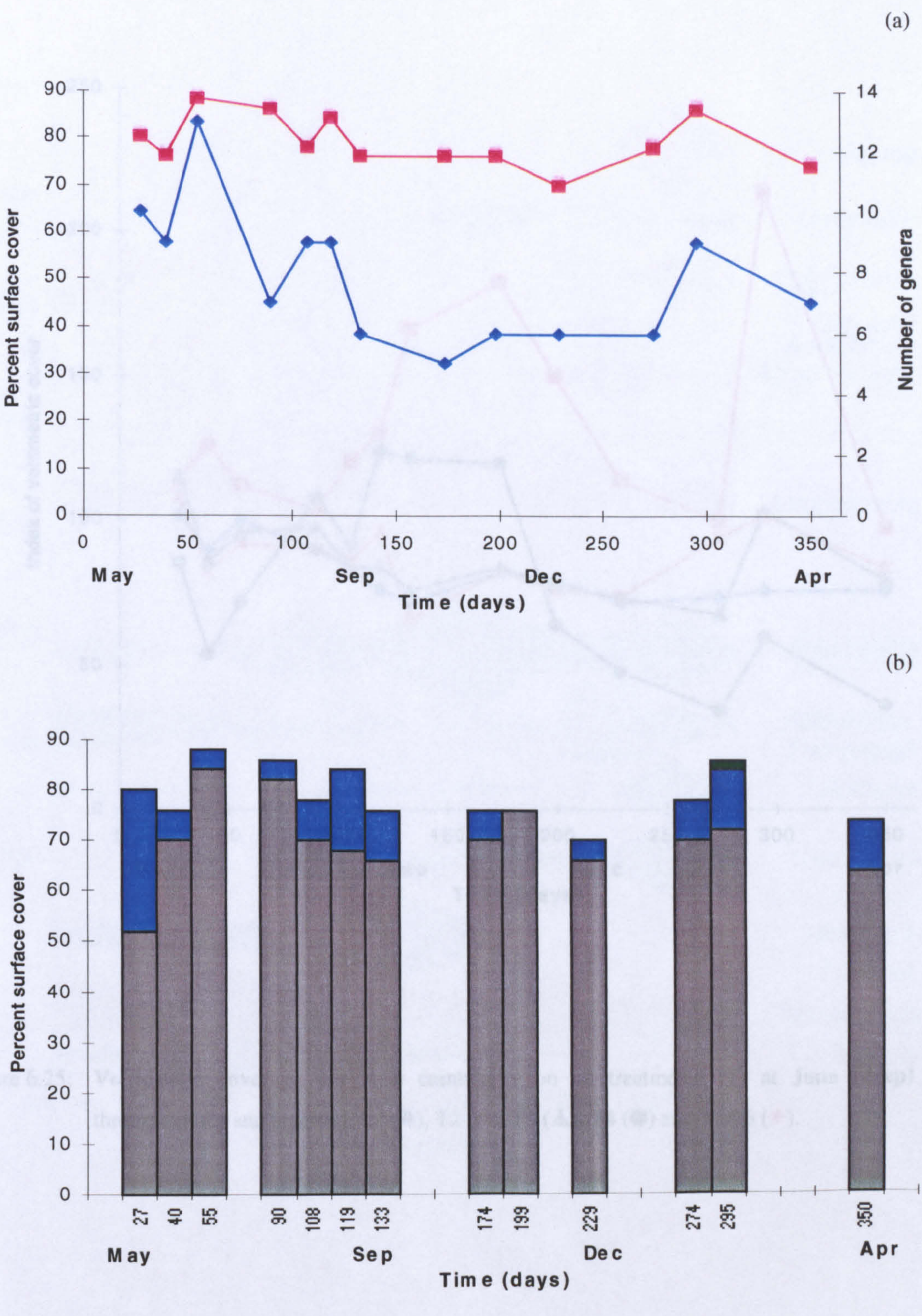


Figure 6.24: Composition and structure of the algal community on **Treatments 5 & 6** (pooled) at **Jana (deep)**; (a) **number of genera** (◆) and total **percent surface cover** (■), (b) total percent surface cover of different **size classes**, SC 1 (■), SC 2 (■), SC 3 (■).

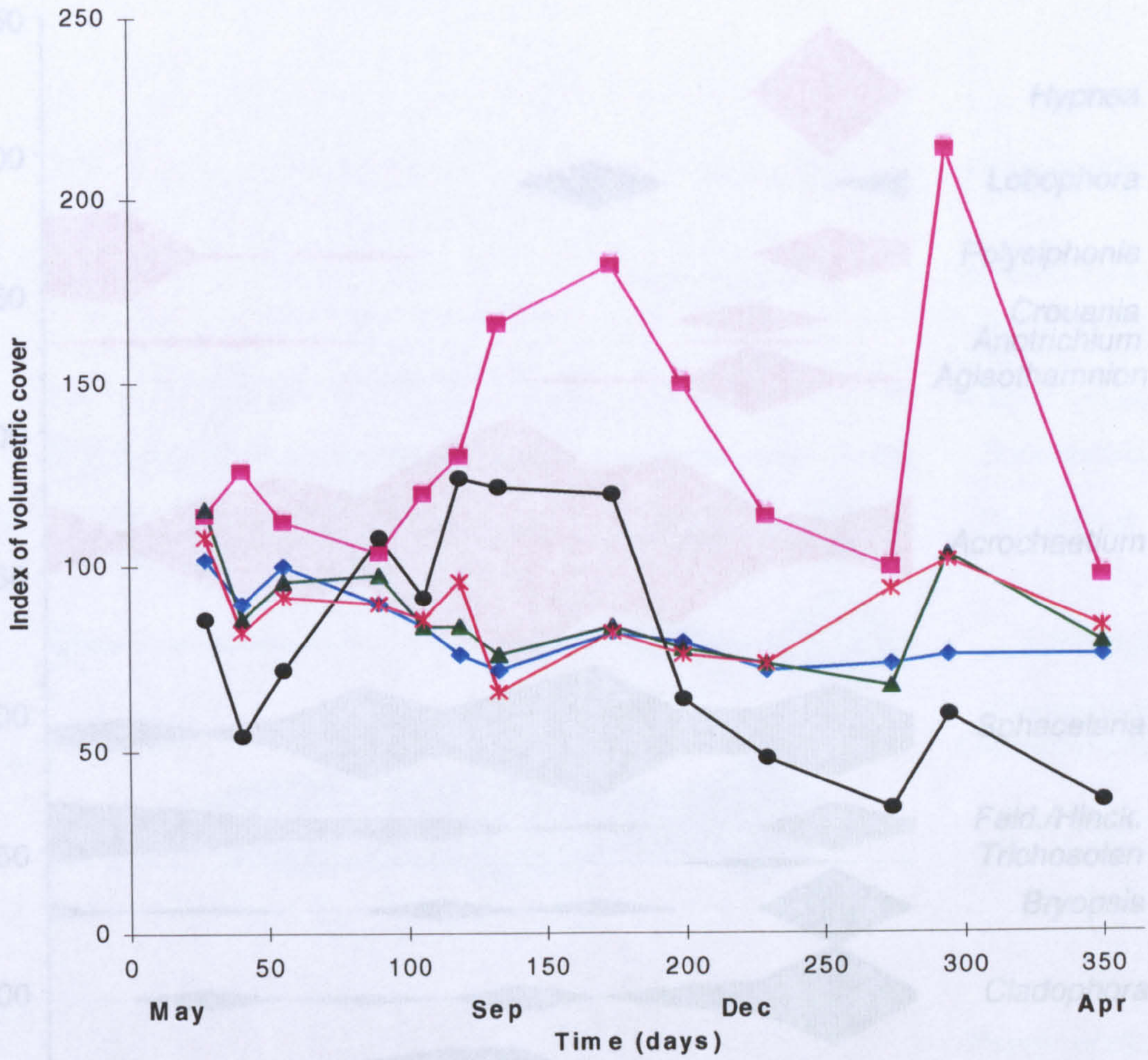


Figure 6.25: **Volumetric cover** of the algal community on all treatments (T) at **Jana (deep)** throughout the study period; T1 (◆), T2 (■), T3 (▲), T4 (●) and T5&6 (✳).

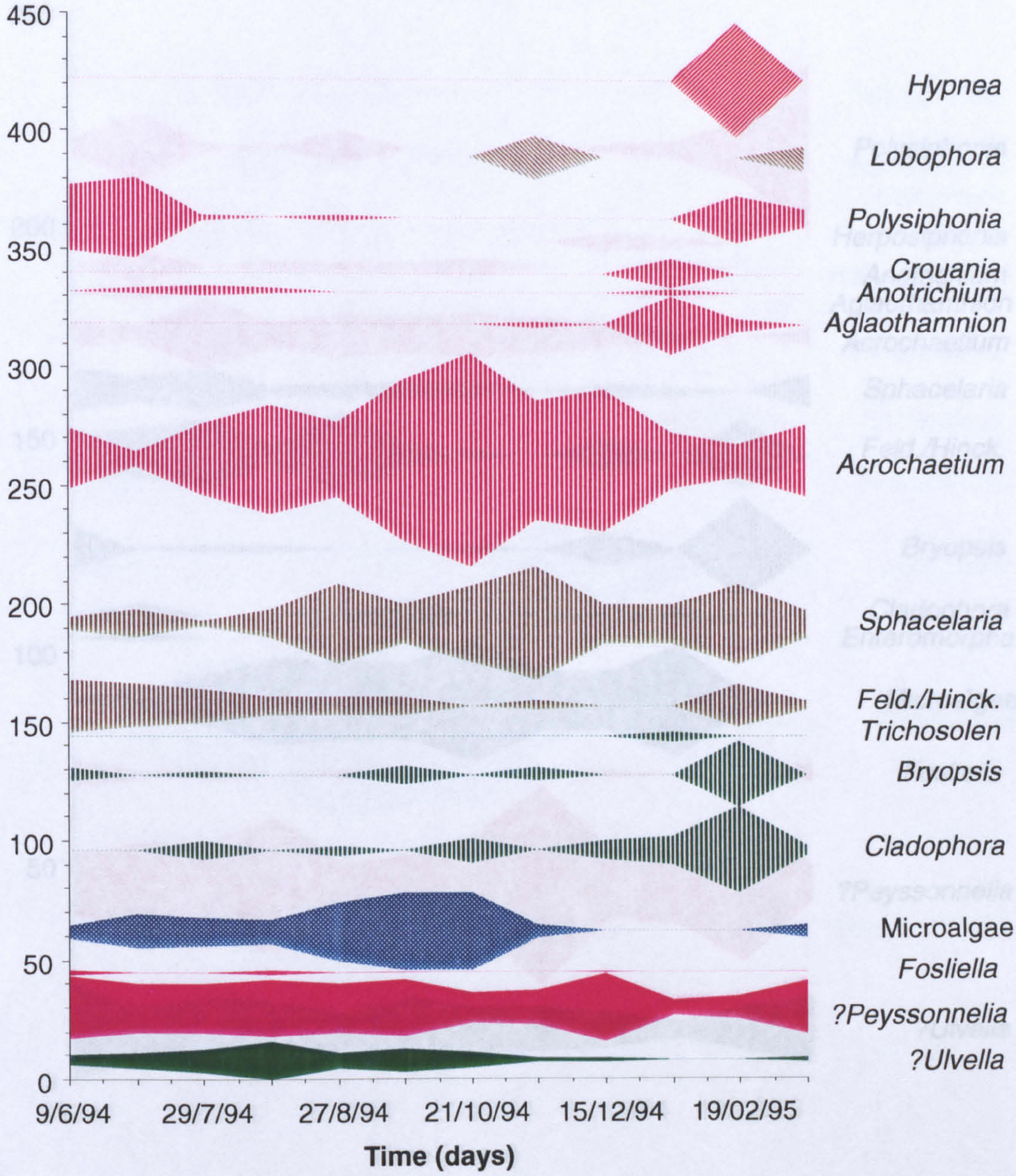


Figure 6.26: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 2** at **Jana (deep)** throughout the study period.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

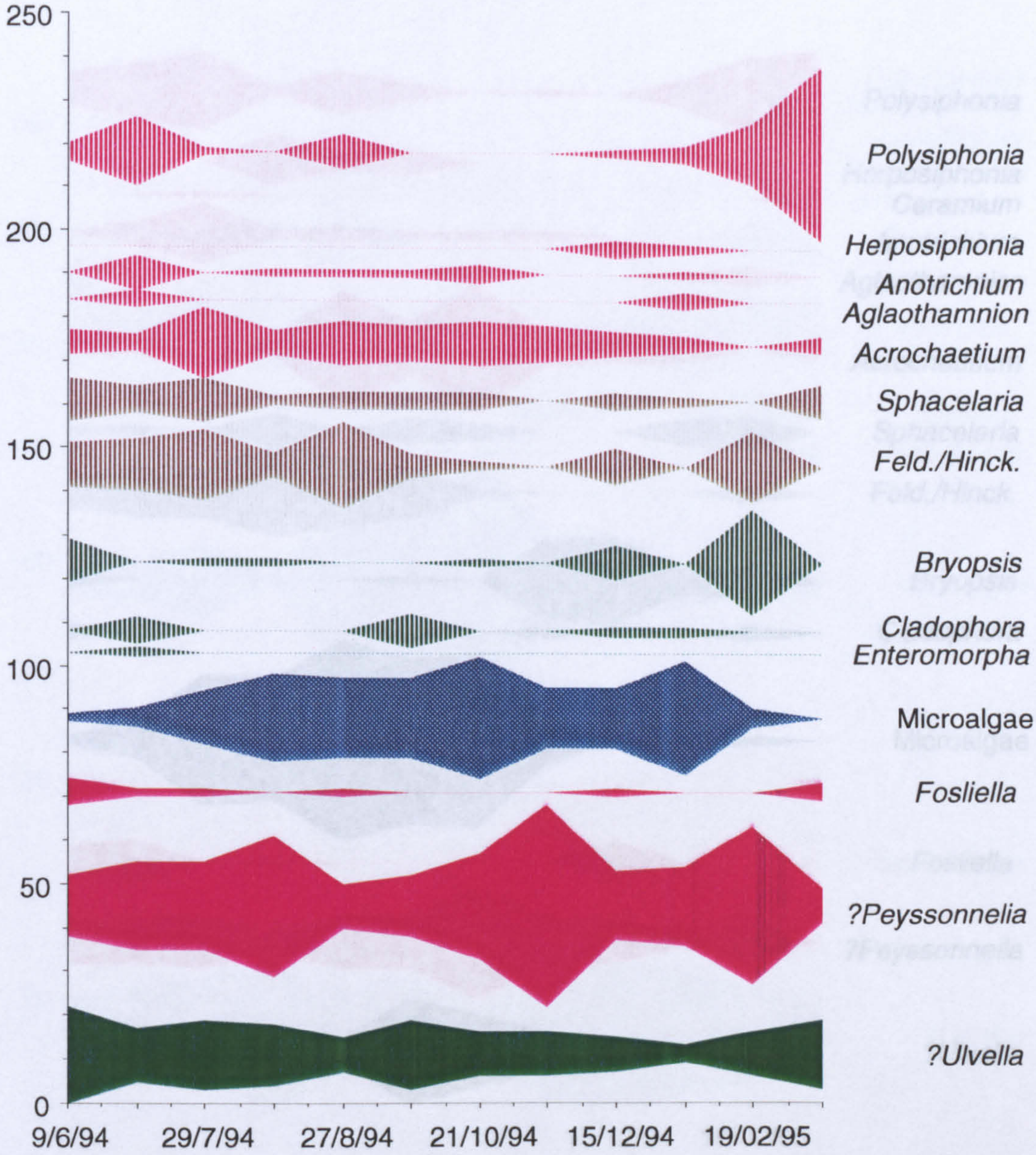


Figure 6.27: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 3** at **Jana (deep)** throughout the study period.

crustose
microalgae
filamentous
corticated-foliose
corticated macrophytes
articulated calcareous
Chlorophyta
Phaeophyta
Rhodophyta

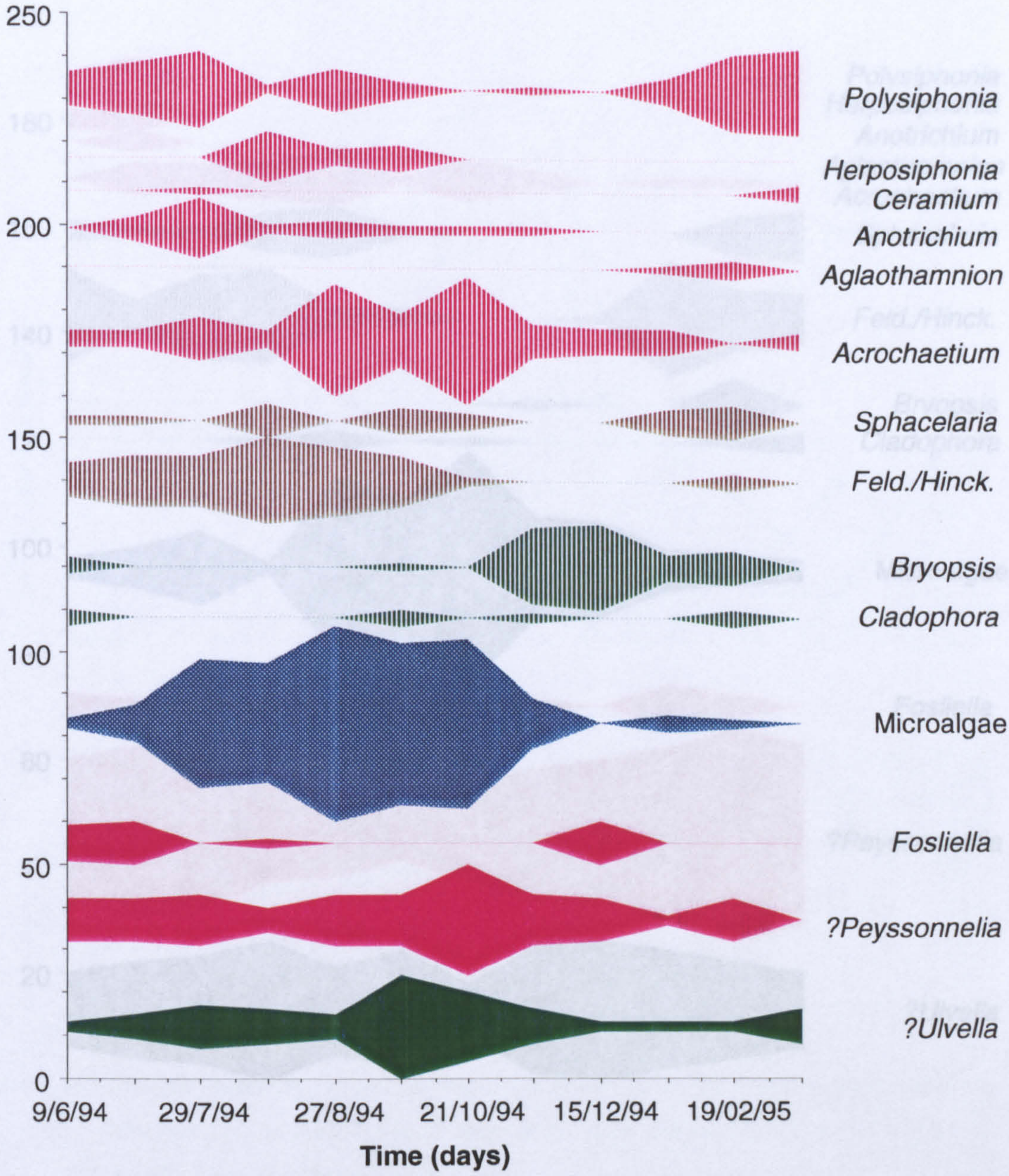


Figure 6.28: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatment 4** at **Jana (deep)** throughout the study period.

crustose | microalgae | filamentous
corticated-foliose | corticated macrophytes | articulated calcareous
Chlorophyta | Phaeophyta | Rhodophyta

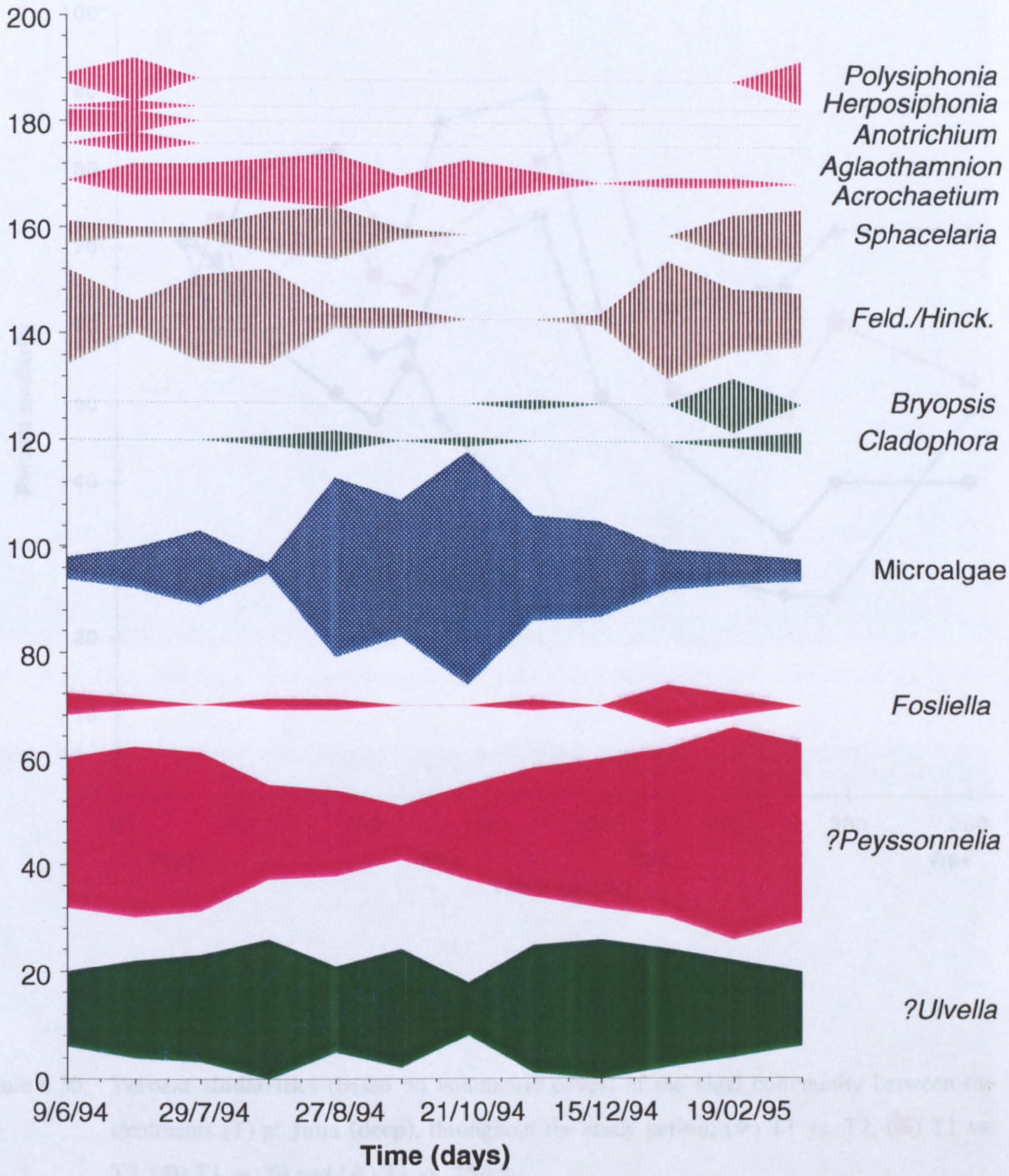


Figure 6.29: **Seasonal patterns** in total volumetric cover per genus recorded on **Treatments 5 & 6** (pooled) at **Jana (deep)** throughout the study period.

crustose	microalgae	filamentous
corticated-foliose	corticated macrophytes	articulated calcareous
Chlorophyta	Phaeophyta	Rhodophyta

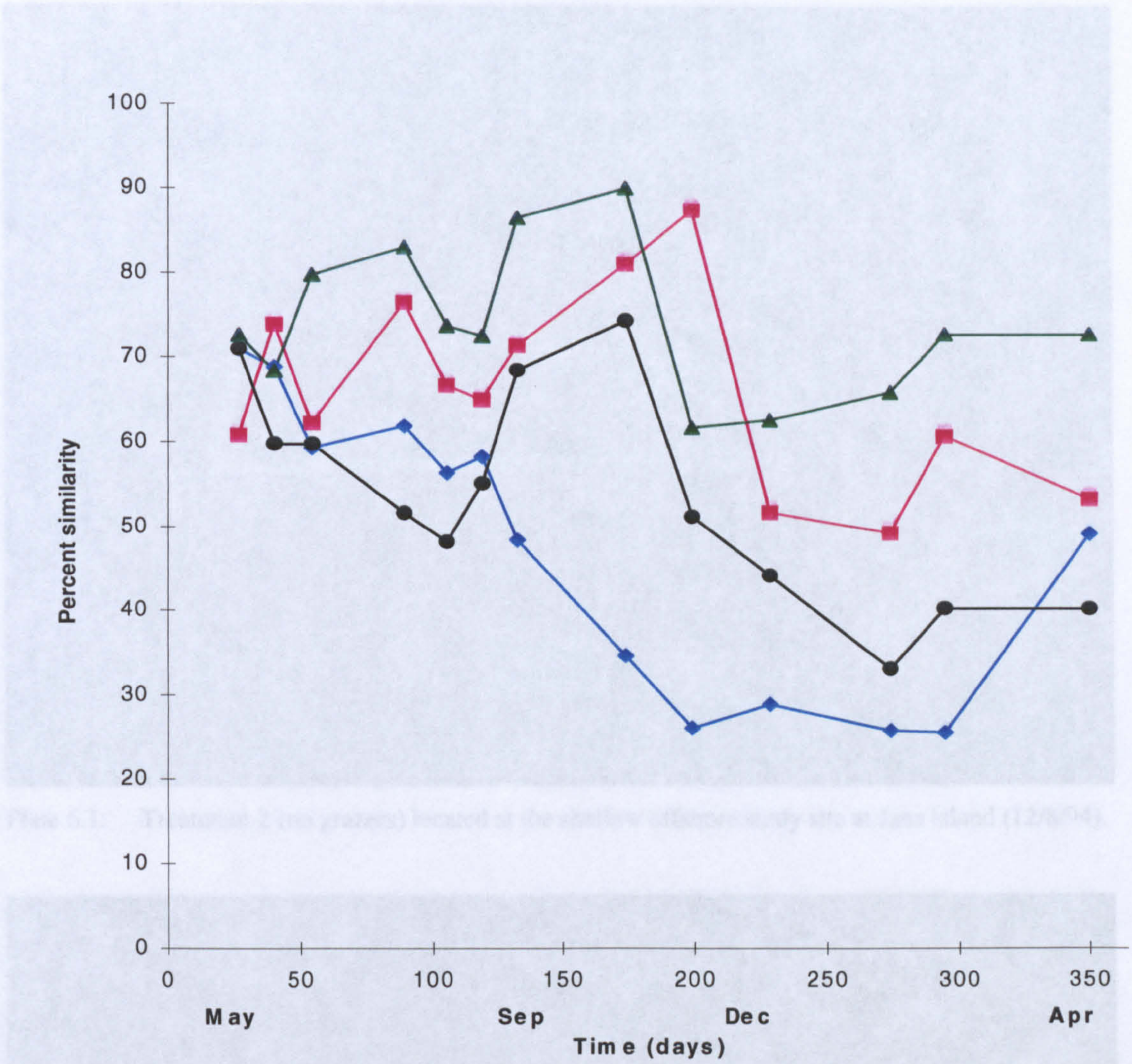


Figure 6.30: **Percent similarities** (based on volumetric cover) of the algal community between the treatments (T) at **Jana (deep)**, throughout the study period; (◆) T1 vs. T2, (■) T1 vs. T3, (●) T1 vs. T4 and (▲) T1 vs. T5&6.

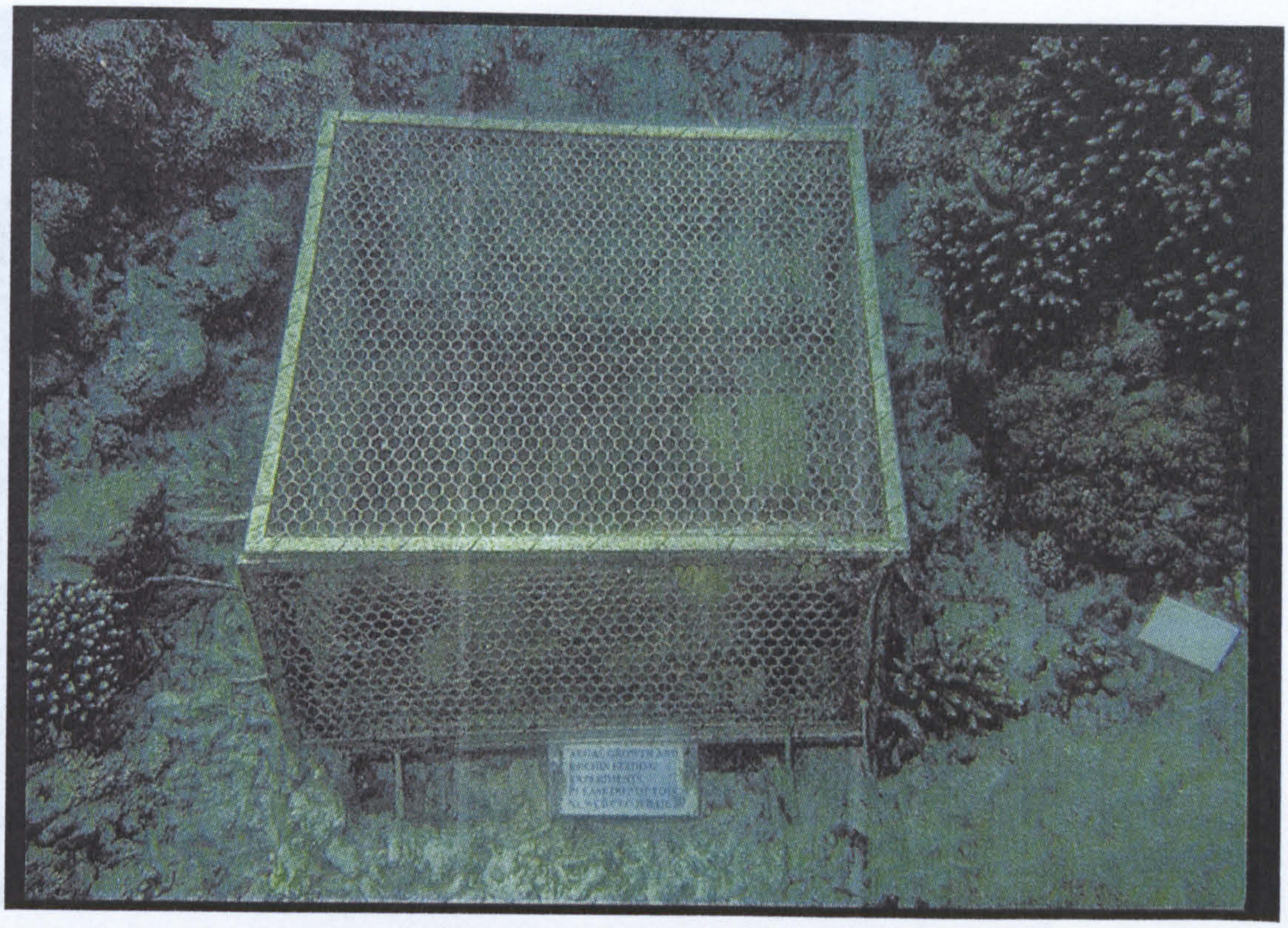


Plate 6.1: Treatment 2 (no grazers) located at the shallow offshore study site at Jana island (12/8/94).

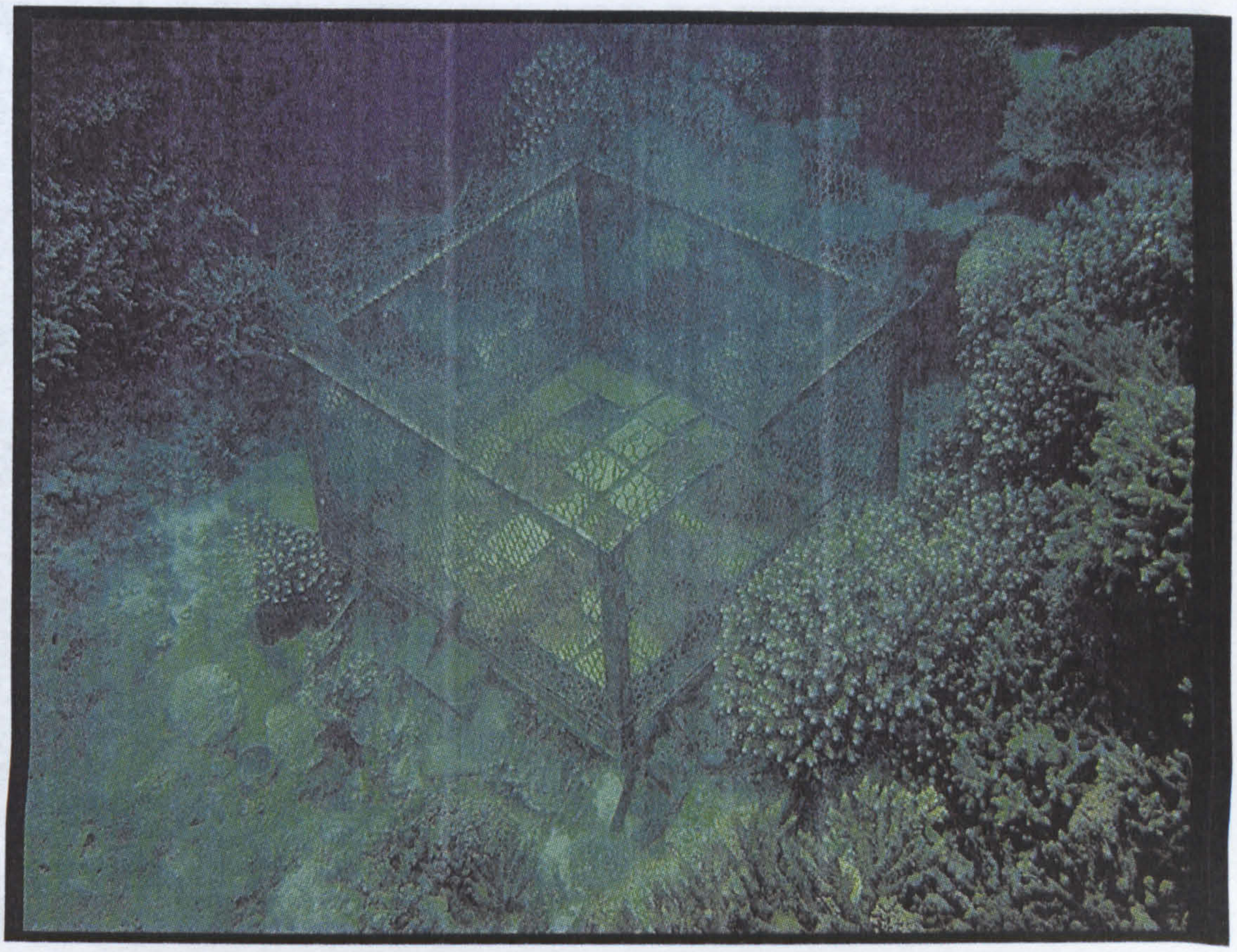


Plate 6.2: Treatment 3 (fish only) located at the shallow offshore study site at Jana island (12/8/94).

Plate 6.3: Treatment 4 (urchins only) located at the shallow inshore study site at Abu Ali (8/94).

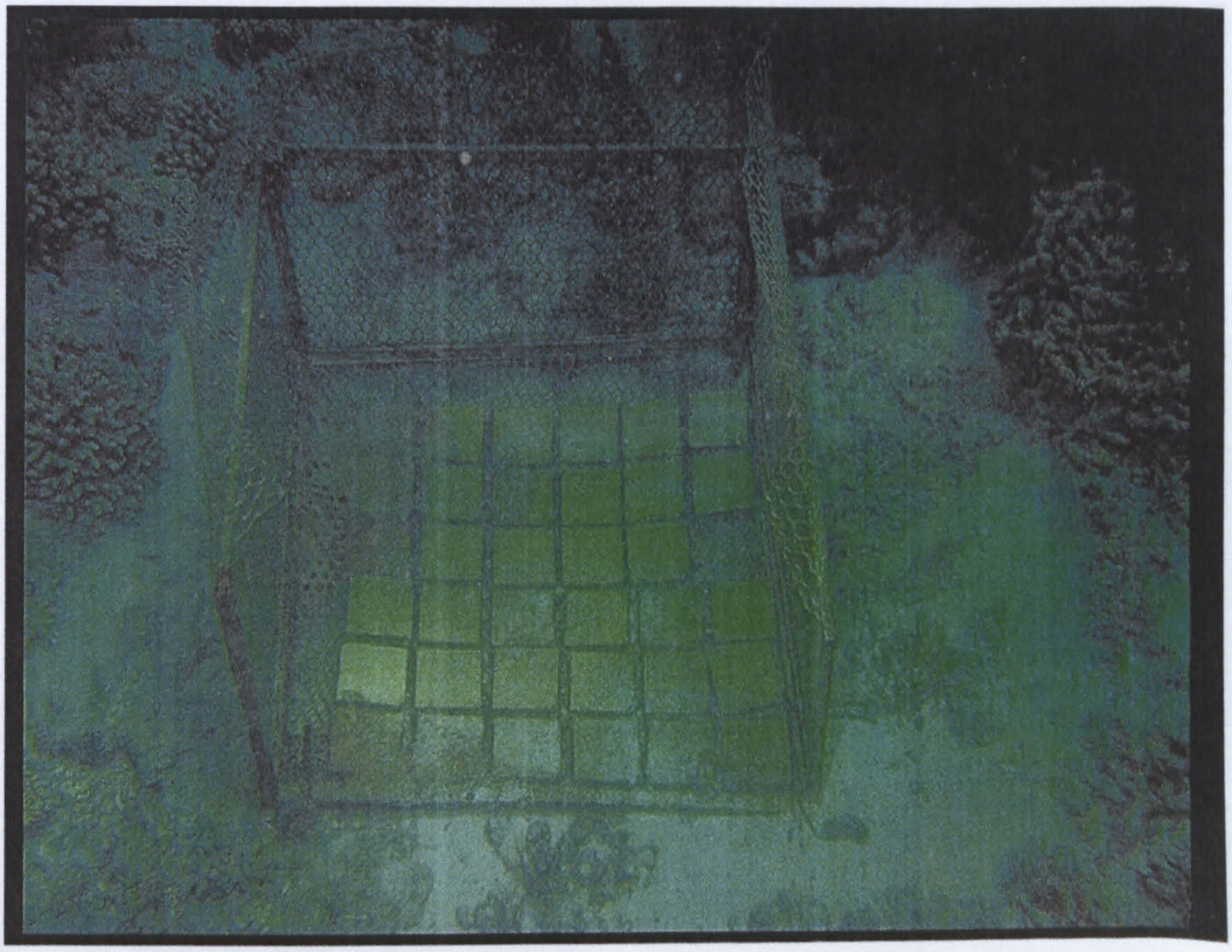


Plate 6.4: Treatment 5 (control) located at the shallow offshore study site at Jana island (12/8/94).

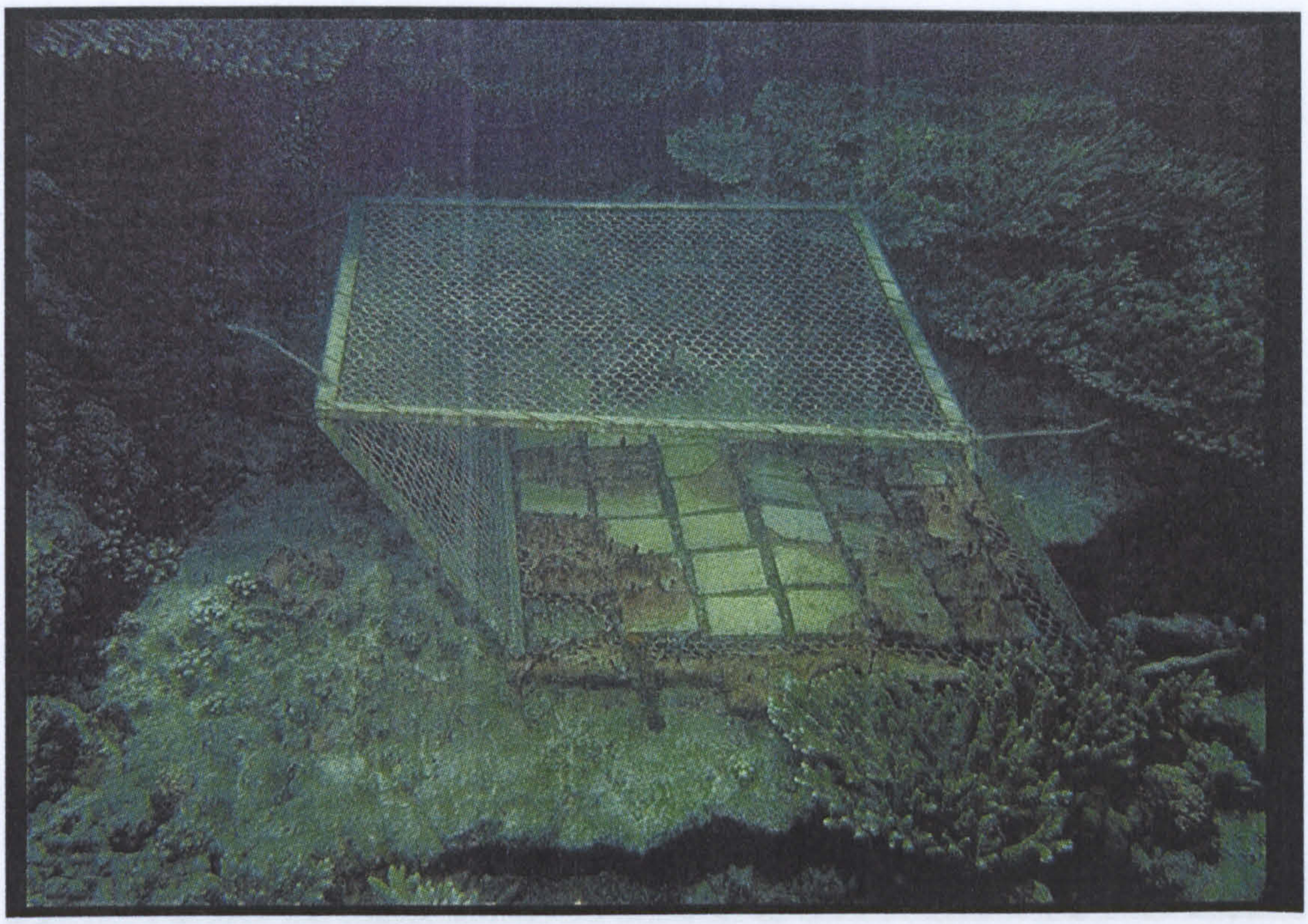


Plate 6.5: Treatment 6 (control) located at the shallow offshore study site at Jana island (12/8/94).

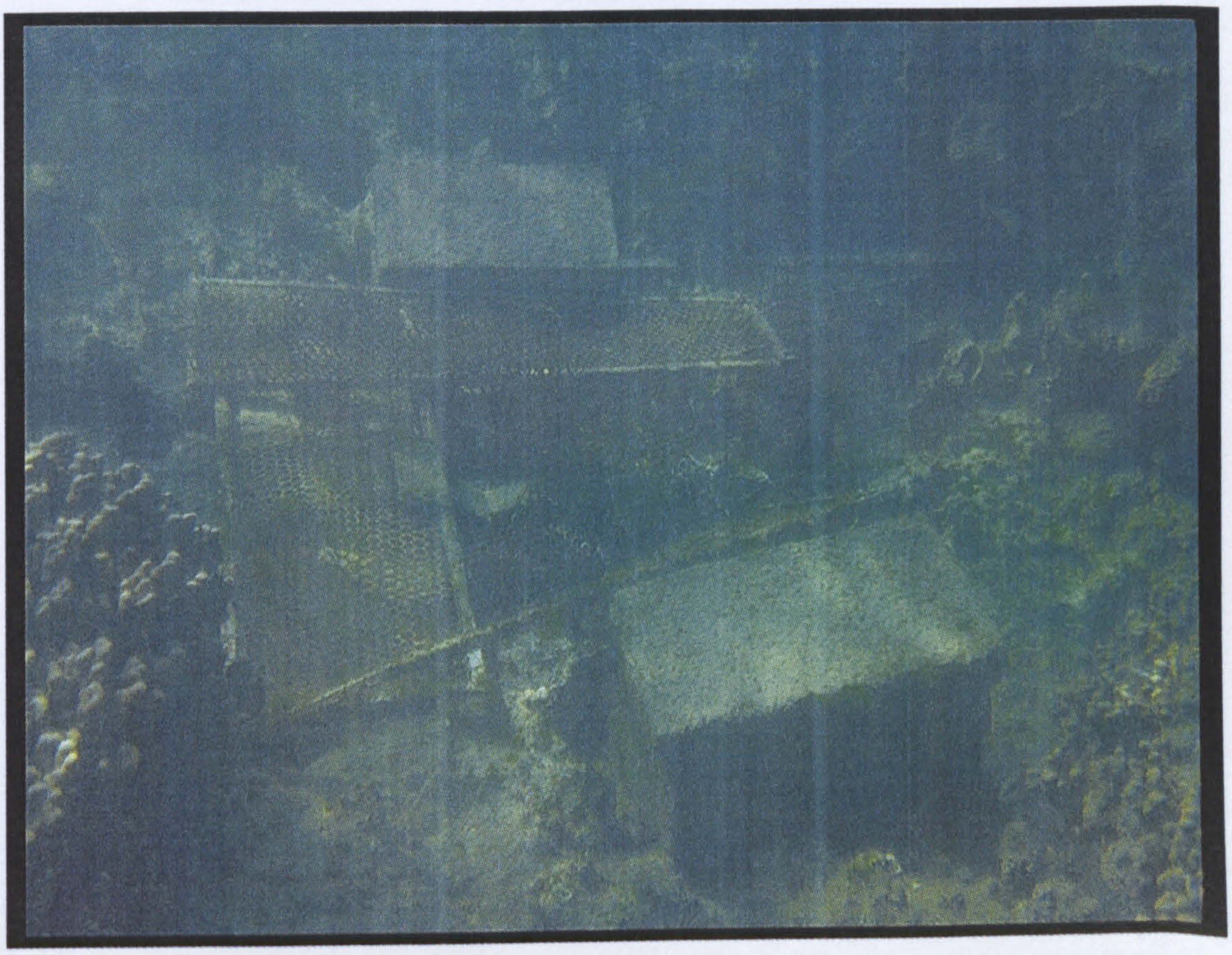


Plate 6.6: Treatment 2 (no grazers) located at the shallow inshore study site at Abu Ali destroyed by storm damage(8/94).

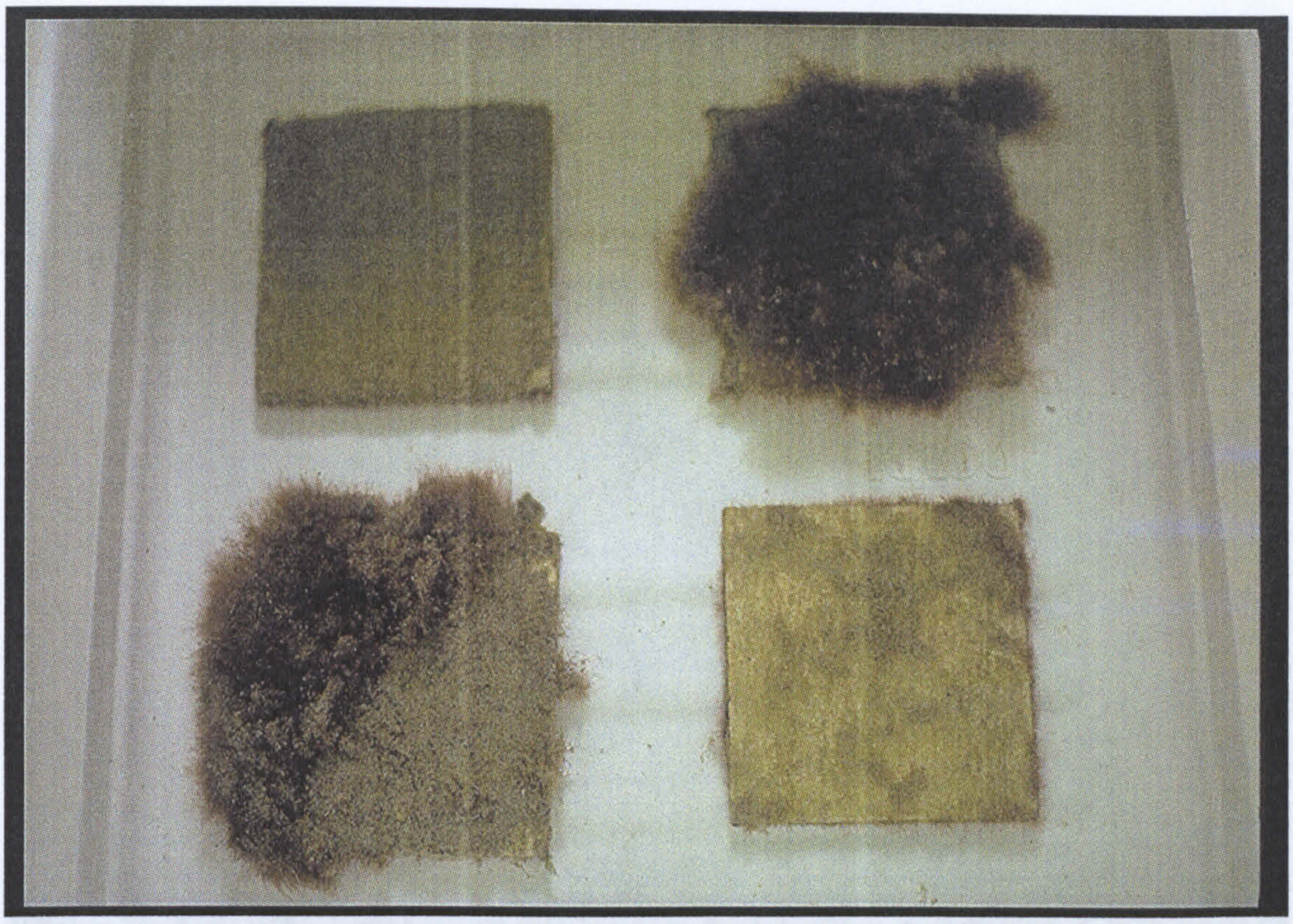


Plate 6.7: Settlement plates from exclusion treatments at Abu Ali, from left to right; T1 and T2 (top row), T3 and T4 (bottom row) (7/94).

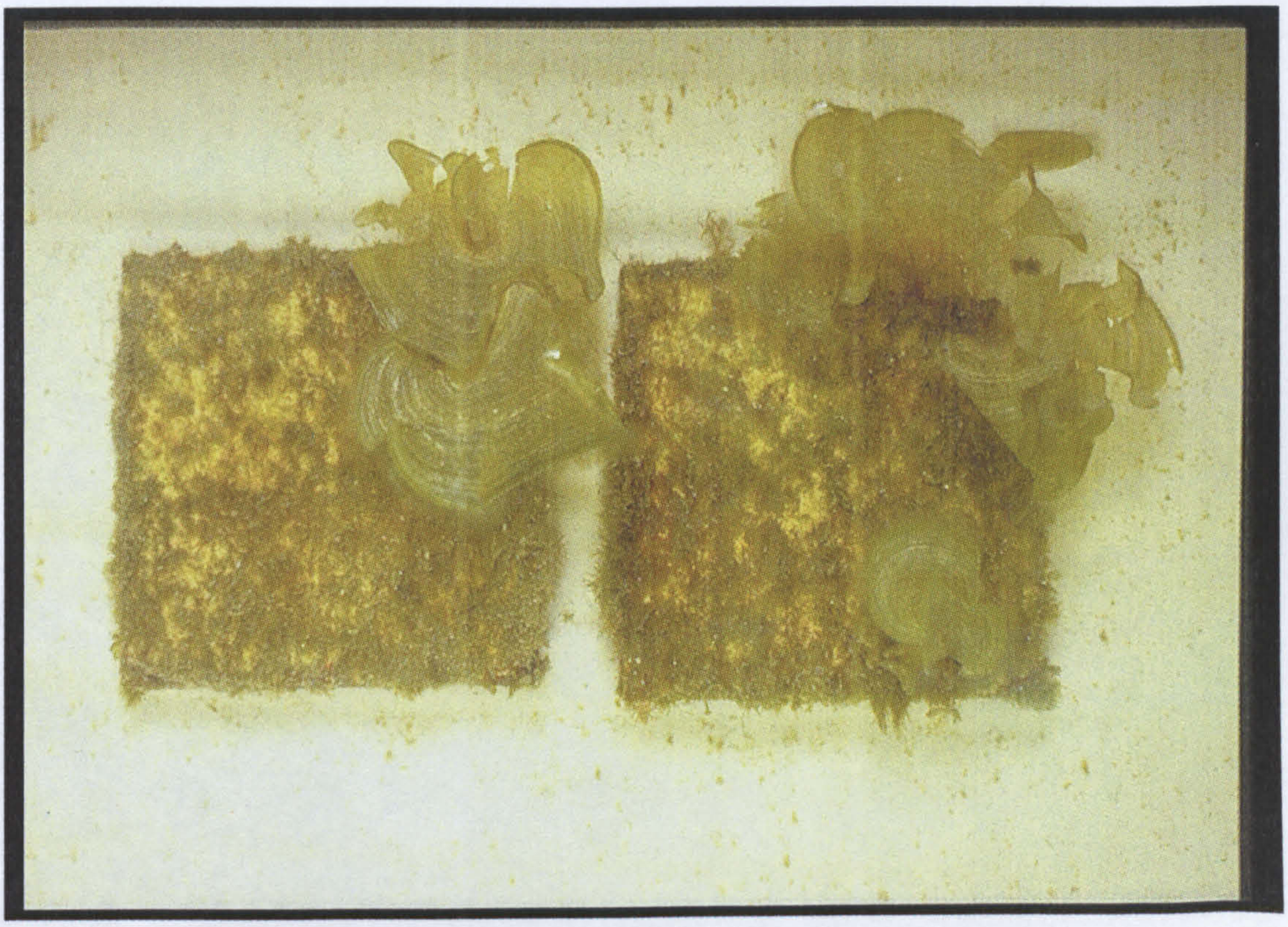


Plate 6.8: Settlement plates (washed) from treatments at Abu Ali showing patchy distribution of *Padina* sp. across the plate surface (13/4/95).

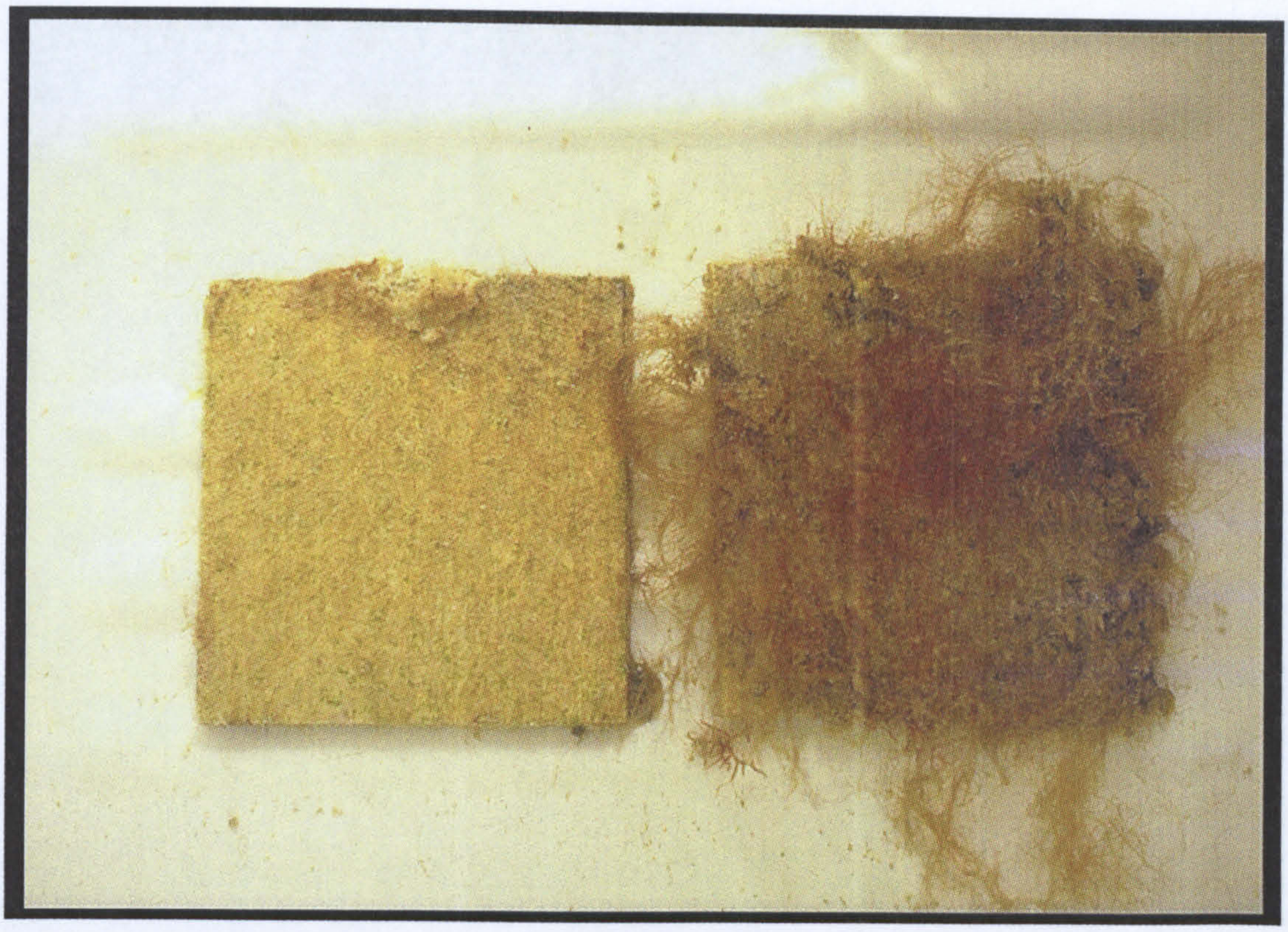


Plate 6.9: Settlement plates from exclusion treatments at Jana (shallow), from left to right; T1 and T2 (with large standing crop of *Polysiphonia* sp.) (12/8/94).

Plate 6.10: Settlement plates from exclusion treatments at Jana (shallow), from left to right; T1 and T2 (with expanding colonies of *Hypnea* and *Lobophora* sp.) (29/1/95).

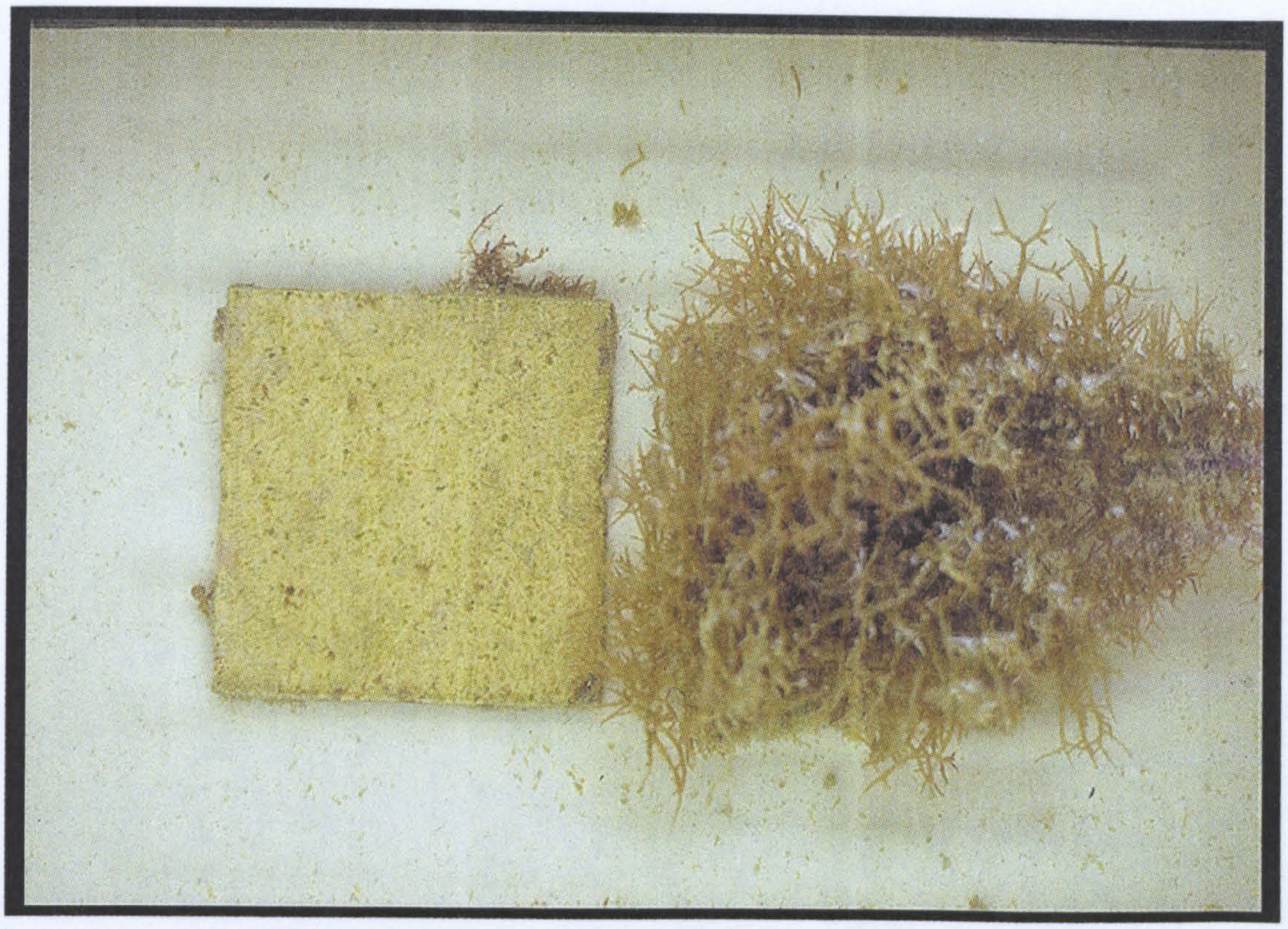


Plate 6.11: Settlement plates from exclusion treatments at Jana (shallow), from left to right; T1 and T2 (with large standing crop of *Hypnea* sp.) (15/4/95).

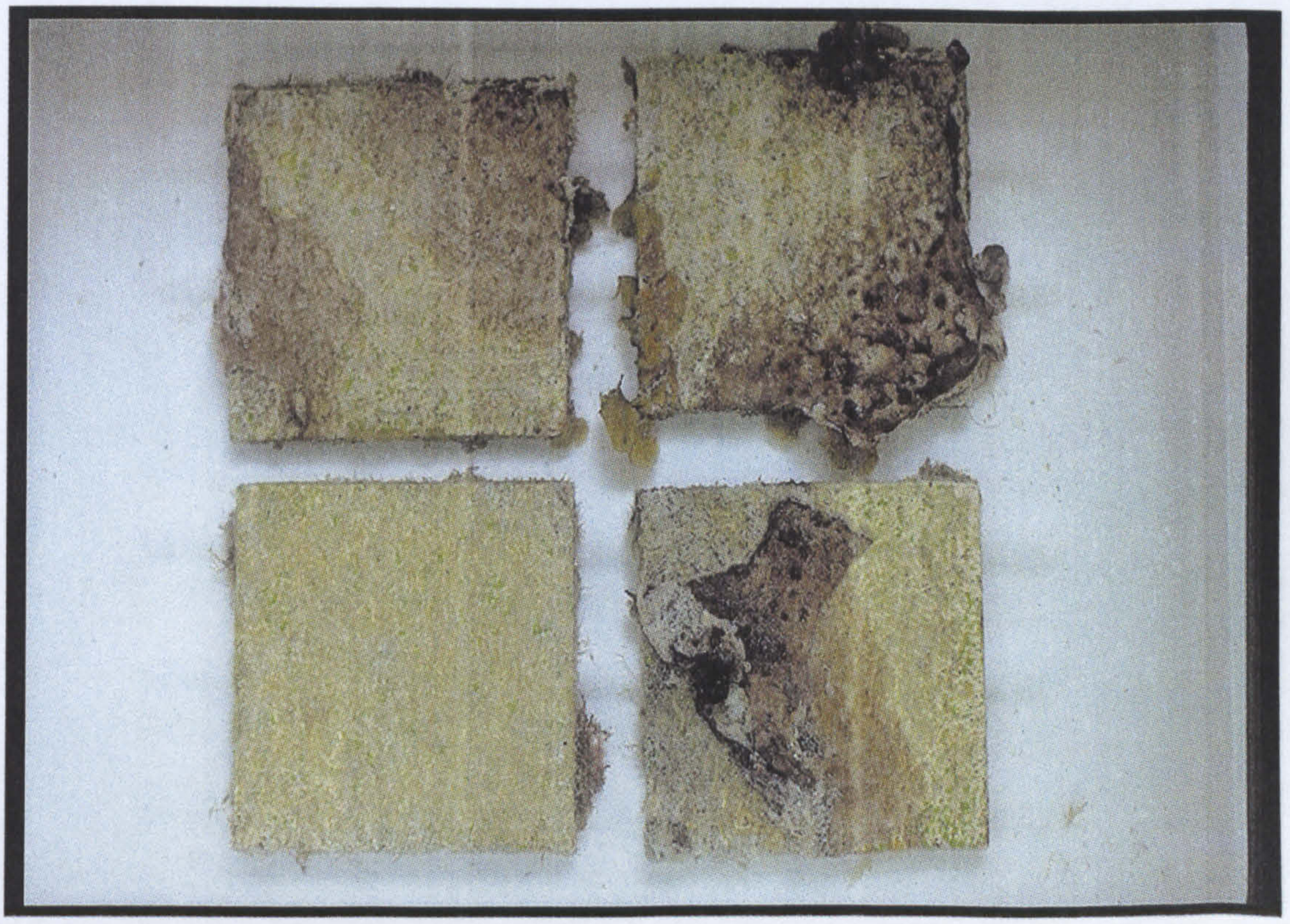


Plate 6.12: Settlement plates from exclusion treatments at Jana (shallow), from left to right; T1 and T3 (both rows). Note seasonal cover by microalgae (29/7/95).

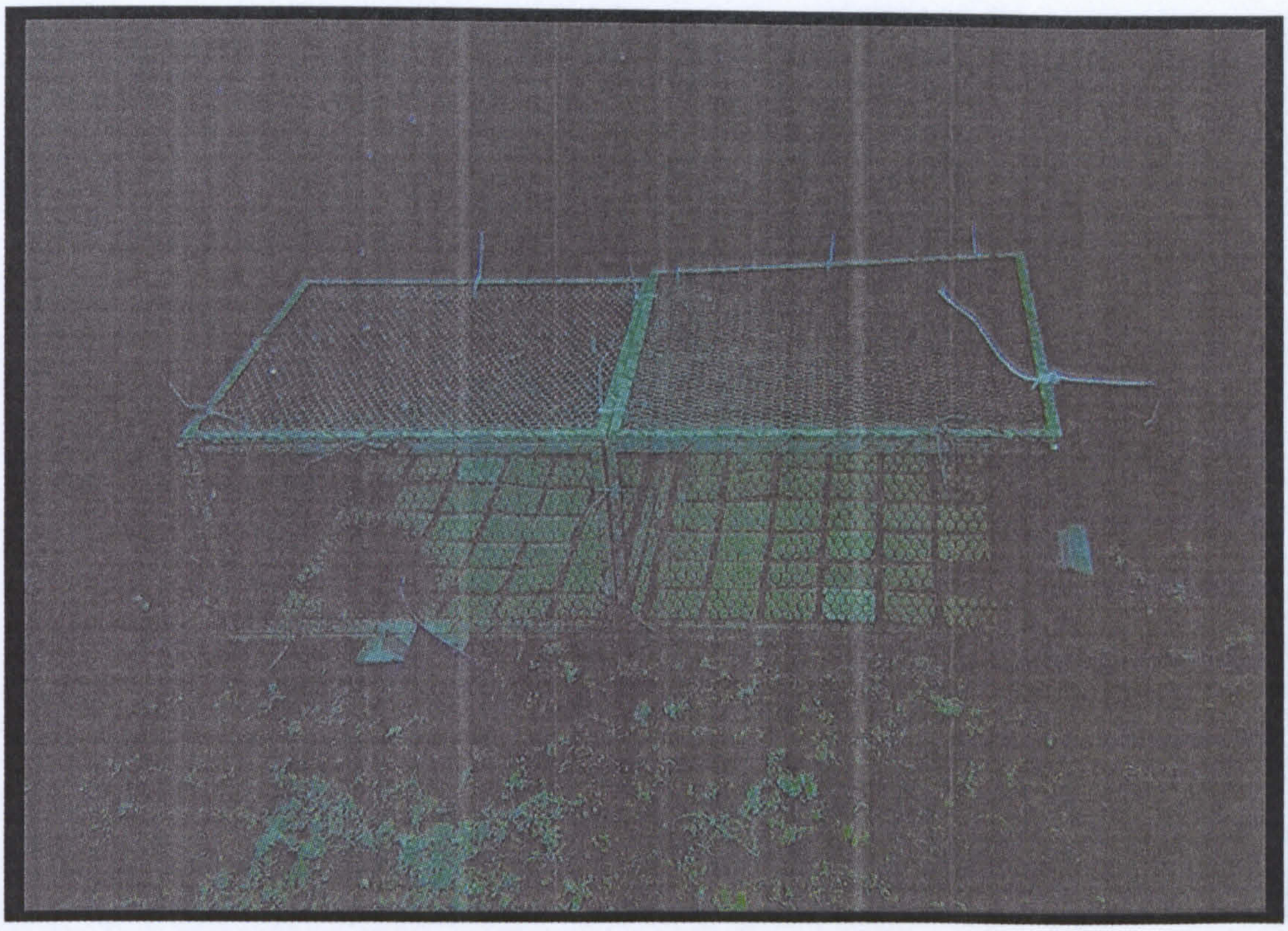


Plate 6.13: Combined Treatment 4 (urchins only) located at the deep offshore study site at Jana Island (14/8/94).

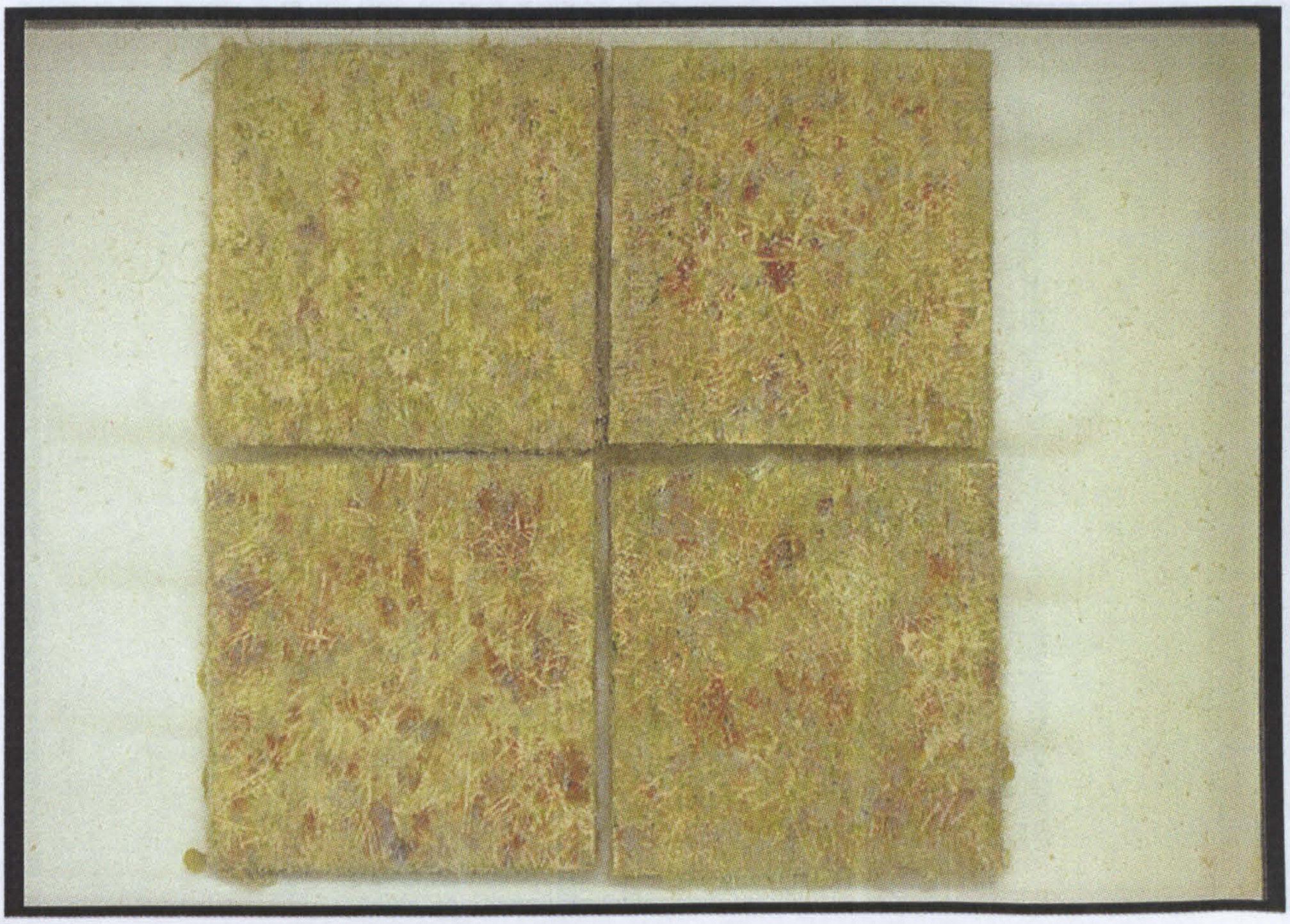


Plate 6.14: Settlement plates (washed) from exclusion treatments at Jana (deep), from left to right; T1 and T5/6 (both rows) (15/4/95).

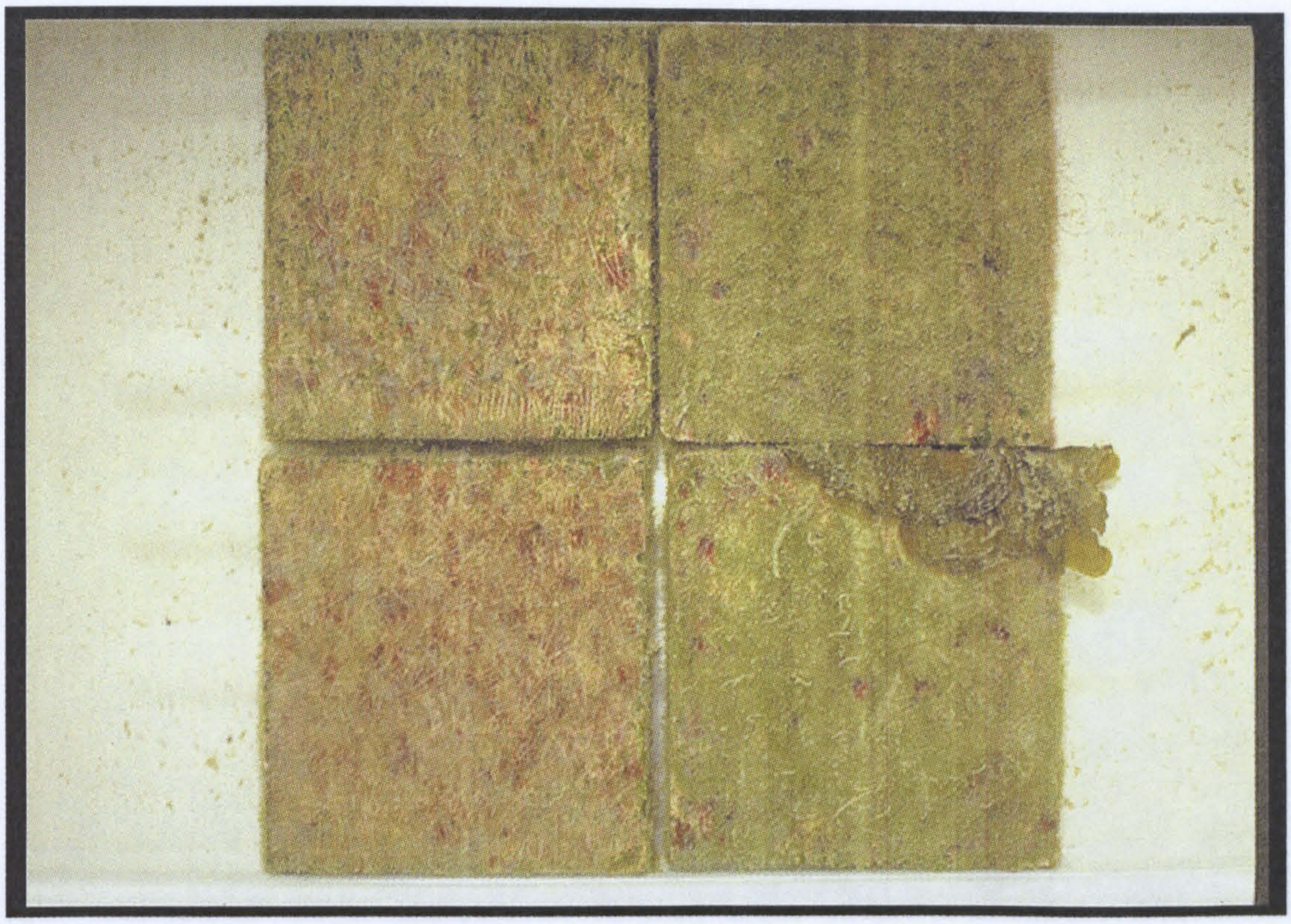


Plate 6.15: Settlement plates (washed) from exclusion treatments at Jana (deep), from left to right; T1 and T2 (both rows) (15/11/95).

Plate 6.16: Settlement plates (washed) from exclusion treatments at Jana (deep), from left to right; T3 and T4 (both rows), with similar algal cover between treatments (15/11/95).

Plate 6.17: Settlement plates (washed) from exclusion treatments at Jana (deep), from left to right; T3 and T4 (both rows), with a reduced algal cover on the latter treatment (29/1/95).

Plate 6.18: Variability in algal growth between settlement plates (washed) from treatments at Abu Ali: *Colpomenia sinuosa* (bottom right) amongst a predominantly filamentous community (15/3/95).

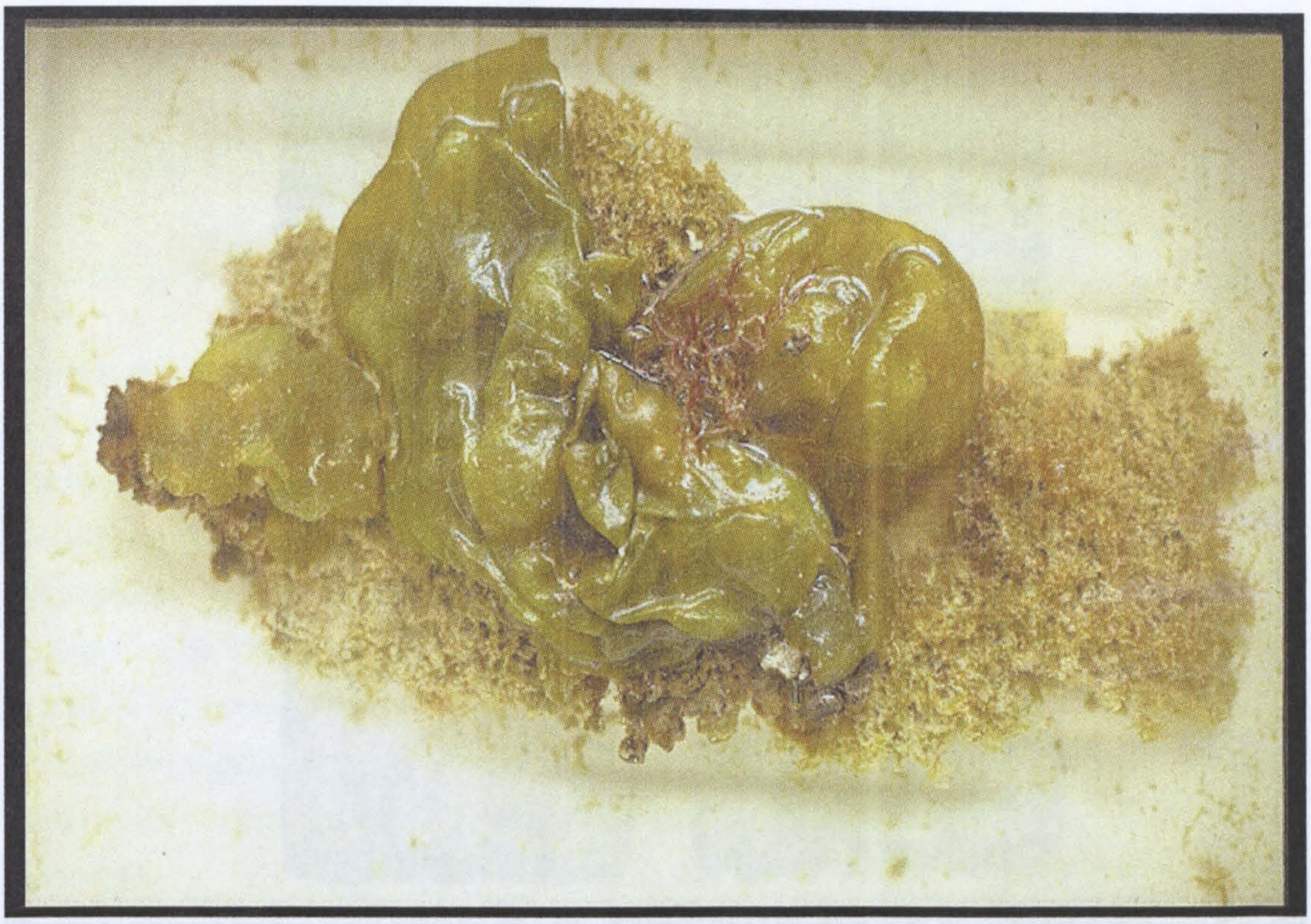


Plate 6.19: Variability in algal growth between settlement plates from Treatment 2 at Jana (shallow): a mixed community of *Hypnea* sp. and *Colpomenia sinuosa* (15/4/95). Compare with Plate 6.13.

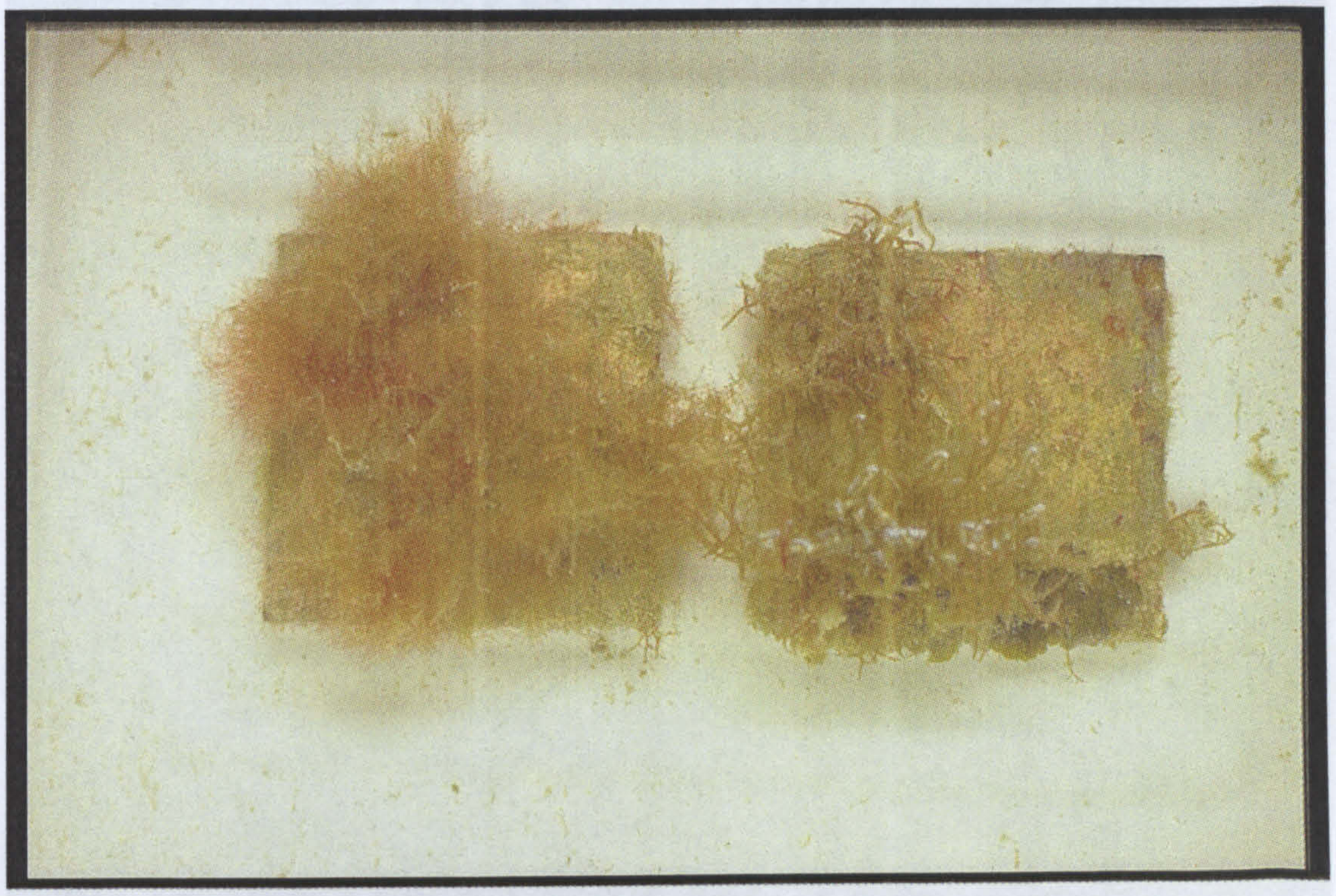


Plate 6.20: Variability in algal growth between settlement plates (washed) from Treatment 2 at Jana (shallow): predominant coverage by either *Polysiphonia* (left) or *Hypnea* (right) (15/4/95).

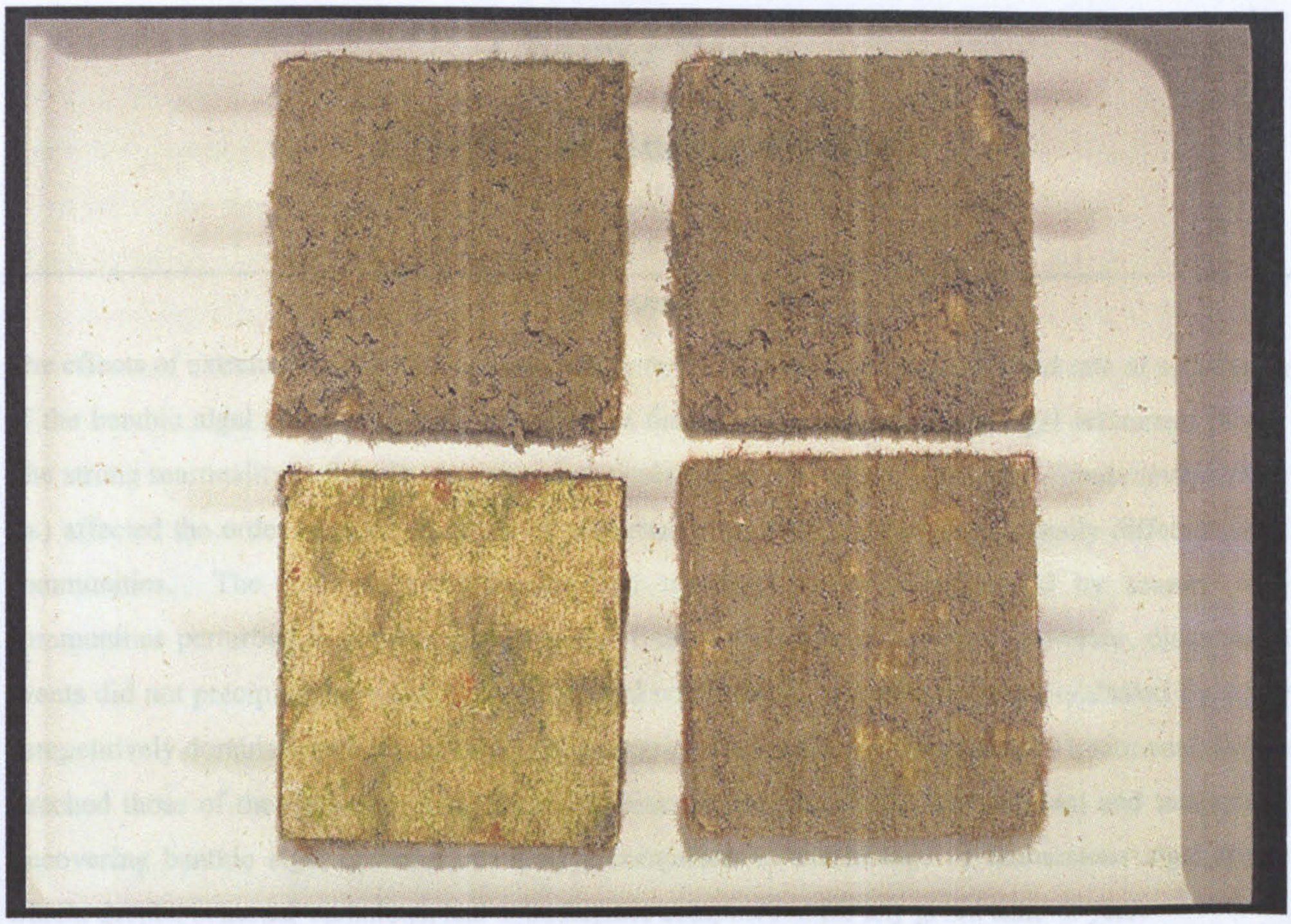


Plate 6.21: Settlement plates from Treatment 1 at Abu Ali where bottom left shows intense grazing by *E. mathaei* (7/9/94).

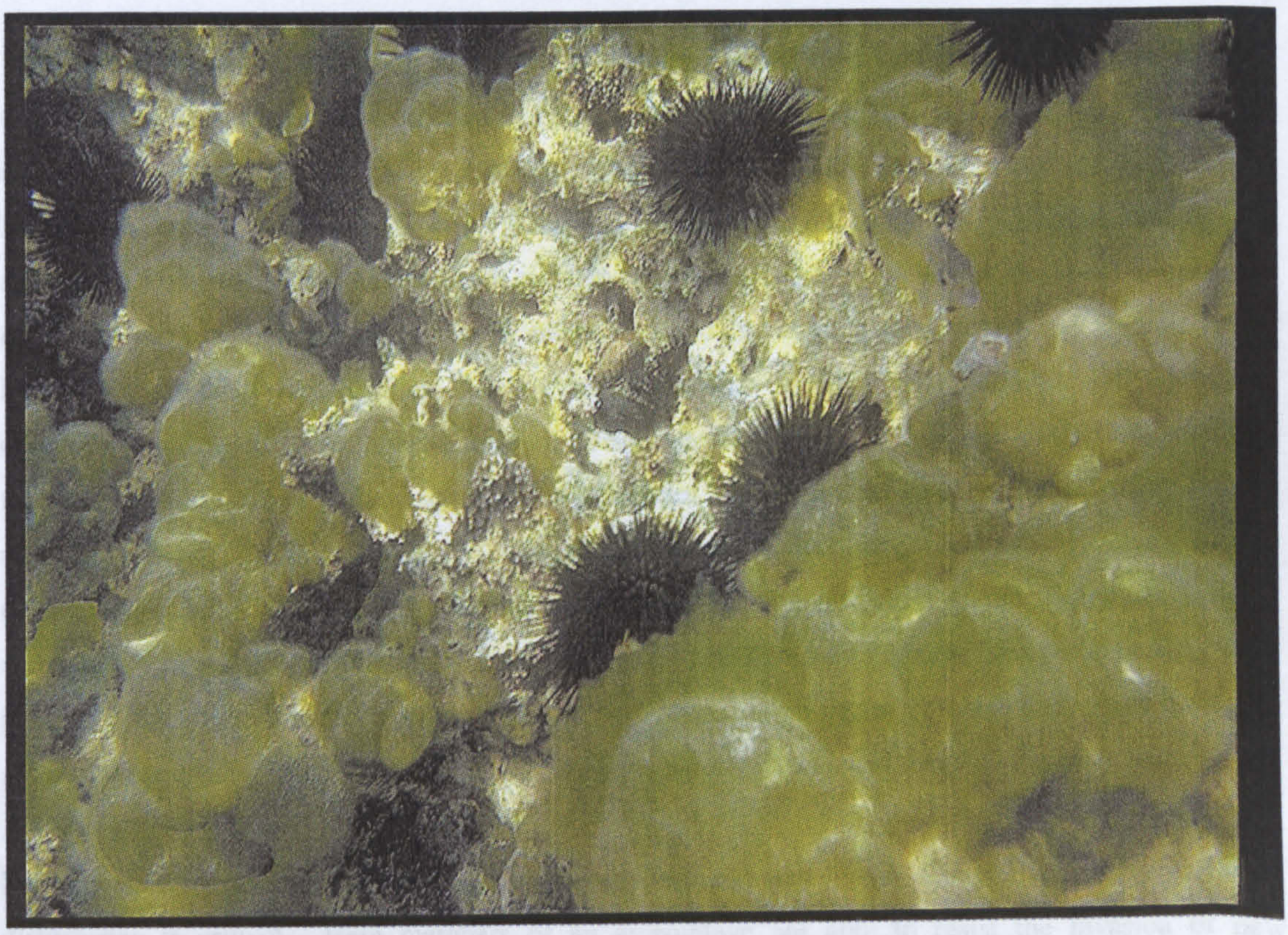


Plate 6.22: Reduction of macroalgae cover (mainly *Colpomenia sinuosa*) due to grazing by *E. mathaei* at Abu Ali (2/2/95).

Chapter Seven

Effects of perturbation

Summary

The effects of extreme perturbation events (total removal of algae) on the pattern and rate of succession of the benthic algal community were examined at the inshore study site using algal settlement plates. The strong seasonality in the life-histories of particular algae (i.e. microalgae and *Feldmannia/Hincksia* sp.) affected the order of re-colonisation of perturbed areas, that resulted in seasonally different algal communities. The rate of re-colonisation and recovery was also influenced by season, with communities perturbed in winter recovering five times faster than in summer. However, disturbance events did not precipitate any alternate stable algal communities (i.e. permanently dominated by a few competitively dominant genera), as subsequent generic compositions of the perturbed treatments always matched those of the controls. Any generic dominance and abundance was seasonal and temporary. Recovering benthic algal communities always comprised an assemblage of filamentous algal forms which, despite seasonal variations, had a predictable composition for any given time of year.

7.1 Introduction

The traditional concept of ecological succession, originally developed for terrestrial plant communities, was that species colonising an available habitat followed a predictable pattern of progression that ultimately resulted in a climax community, dominated by a few competitively superior species. Numerous studies have investigated, theoretically and experimentally, the different models and mechanisms that have been advanced to describe the processes by which observed community structures and assemblages are produced and maintained (for review see Connell and Slatyer, 1977). For terrestrial plant communities, limiting resources such as light, soil nutrients and water, are competitively exploited by species with differing life-histories and resource allocation strategies (Tilman, 1990). Although these approaches have been applied to marine communities (see McCook and Chapman, 1991), Underwood and Anderson (1994) argue that since the constraints facing marine organisms are often different to those of terrestrial plants, such applications are inappropriate. Instead, mechanisms of succession for marine organisms should be based on their abilities for exploiting their particular limiting resource. For most sessile organisms, the ability to colonise and secure available substratum is critical, either by settling and overgrowing other species or resisting their invasion.

For one mechanism in particular, termed the *inhibition* model (*sensu* Connell and Slatyer, 1977), disturbance is critical. Here members of an assemblage are able to resist the invasion of new individuals until a disturbance event makes the limiting resource available for colonisation (Sutherland and Karlson, 1977; Sousa, 1979a,b). However, while some marine studies have found evidence to

support the notion of a predictable process of succession in marine assemblages (Sousa, 1979a,b; Farrell, 1991; McCook and Chapman, 1991,1993), others have observed marine communities where no apparent succession and predictable outcome occurs (Sutherland and Karlson, 1977; Breitburg, 1985). Furthermore, the timing of the disturbance event that makes colonising space available has important effects when involving communities whose inhabitants' life-histories are strongly affected by season (Sutherland and Karlson, 1977; Osman, 1978; Keough, 1983; Farrell, 1991; Turner and Todd, 1993). In such cases, different patterns of succession can occur, resulting in alternative, stable communities (Underwood and Anderson, 1994).

The aim of this study was to investigate the impact of an extreme perturbation event on the rates and patterns of succession and the subsequent composition and stability of the benthic algal community. The perturbation experiment was undertaken on the inshore fringing reef at Abu Ali and took the form of total removal (scraping) of algal growth from settlement plates. Such an event might be likened to intensive grazing by herbivorous fish and/or urchins.

7.2 Materials and methods

7.2.1 Experimental design

In June 1994 six algal settlement panels were secured at the inshore study site (four treatments and one replicated control). All panels were in close proximity to each other, in total no more than a few metres apart. The design of the panels was identical to those described in section 5.2.1 except that each panel was 92 cm x 61.5 cm in size and covered with 54 settlement plates (9 x 6 grid). In August 1994, prior to the start of the experiment, the composition of the algal community growing on each of the settlement panels was monitored for two weeks. This was to confirm that each treatment had attained a similar level of algal development.

Perturbation of the settlement plates on each of the treatment panels involved the complete removal of the algal colonies covering two opposing 'quarters' of the tile surface. The *in situ* removal of the algal community was undertaken by hand and the surface of the tiles were scraped as cleanly as could be detected by the naked eye. The remaining two quarters of the plate surface were left intact (Plate 7.1). Re-colonisation of the newly exposed settlement substrate could therefore come from both the settlement of propagules from the water column and/or expansion of existing algal colonies in the unperturbed areas. This prevented the presence of algal species from being a limiting factor as the experiment progressed.

The experiment continued for a total of nine months during which the four treatments were subjected to two periods of perturbation. The first was begun in August 1994, and the second in January 1995. However, in each case, the treatments were not effected simultaneously. Instead perturbation of the

separate treatments was staggered over a two month period (Table 7.1). Hence the overall design of the experiment examined the regenerative ability of the algal community both between seasons (i.e. summer and winter months) and within seasons (i.e. staggered intervals of perturbation between treatments). It is important to note that during the winter months, sampling and perturbation of Treatments 1 and 3 was discontinued due to storm damage.

Sampling was undertaken twice a week during which each plate was randomly selected, the algal community growing upon it investigated (see section 7.2.2), and then replaced in order to keep the surface area available to grazers and re-colonising algae constant. Furthermore, as analysis of the re-colonising community examined only one area of the plate at a time, perturbation of the 54 settlement plates on each treatment resulted in over one hundred possible measurements. Hence when all plates had been examined at least once, they were again individually sampled but this time analysing the opposing perturbed area of the plate. This design allowed the continued effects of the two seasonal investigations (i.e. summer and winter) to be undertaken concurrently. Therefore, once the sampling of the treatments had continued onto the opposing corners of the plates, the previously sampled areas were re-used for the second series of perturbations. It was assumed that the re-occurrence of a perturbation event on a settlement plate would not influence the status of the re-colonising algal colonies on the opposite corner of the plate. It is important to note however, that re-colonisation after the first set of perturbations (i.e. summer) was monitored for a nine month period, while for the second set (i.e. winter) monitoring continued for only four months after the initial perturbation.

7.2.2 Sample and data analysis

The analyses performed were identical to those described in sections 5.2.2 and 5.2.3. It is important to note, however, that the sample area of the plate surface was restricted to the perturbed region currently under examination (i.e. 3.75 cm^2). This also applied to the corresponding unperturbed areas of the replicated controls in order to allow direct comparison of the algal communities per unit of surface area.

It is important to note however, that because the control treatments were replicated while the perturbed treatments were not, calculation of the percent similarity (see section 5.2.3) between the treatments could not be based on pooled values for the control treatment, due to additive effects. Instead the percent similarities were first calculated between the perturbed treatments and each control replicate, and then averaged to produce a single estimate of similarity with the control treatment.

7.3 Results

7.3.1 Similarity prior to perturbation

For the two weeks prior to the first perturbation event, a comparison of the algal communities growing on all treatments was made (Table 7.2). There was no significant difference between the experimental treatments and the control replicates, nor between the replicates, in terms of percent similarity, whether based on generic presence/absence, percent surface cover or volumetric cover. There was also no significant difference in the total number of genera on different treatments. However, in terms of total surface and volumetric cover a significant difference was detected, attributable to a larger surface cover that existed on Treatment 1 (comparison of means, Table 7.3). In addition, a significant decrease in the percent similarity in terms of generic presence/absence and volumetric cover developed between treatments over the two weeks prior to the first perturbation event.

Furthermore, comparison of the control replicates over the entire study period revealed significant differences in terms of total percent surface cover and volumetric cover, but not for the number of genera. Temporally, however, the algal composition varied significantly in terms of the number of genera and volumetric cover only; the former decreased during winter (Figure 7.2), while the latter increased (Figure 7.4). In addition the percent similarity between the control replicates fluctuated throughout the study period (Figure 7.1).

7.3.2 Re-colonisation after perturbation

Number of genera, percent surface cover and volumetric cover were the parameters recorded to describe the algal communities on each treatment before and after perturbation. Storm damage during December prevented further samples being taken from Treatments 1 and 3.

Summer perturbation

After perturbation, the algal communities on Treatments 1-4 all re-attained levels of community composition equivalent to those present on the control replicates, whether in terms of the number of genera (Figure 7.2), total percent surface cover (Figure 7.3) or total volumetric cover (Figure 7.4) (see below). Stages of the re-colonisation process can be seen in Plates 7.3, 7.4 and 7.5. Maximum similarity between all the treatments after the perturbation events occurred during December. Subsequently, however, algal communities on the remaining treatments (i.e. Treatments 2 and 4) exhibited increased variability and dissimilarity. For example, the overall number of genera declined, even amongst the control replicates (Figure 7.2). Furthermore, the volumetric cover on Treatment 3 peaked in February (Figure 7.4) while the percent surface cover on Treatment 4 declined during this period (Figure 7.4).

The similarities of algal genera between the control and perturbed treatments also showed a return to levels equivalent to those recorded between the control replicates, whether in terms of generic presence/absence (Figure 7.5), percent surface cover (Figure 7.6), or volumetric cover (Figure 7.7) (see below). Furthermore, there did not appear to be so clear a divergence from the control treatments as occurred during the winter. However, high variability in community composition occurred during this period (January-March), due to the large fluctuations in percent similarity between the control replicates.

Winter perturbation

After perturbation, algal communities on Treatments 2 (repeat) (2R) and 4 (repeat) (4R) also re-attained levels of community composition equivalent to those supported on the control replicates, whether in terms of the number of genera (Figure 7.8), total percent surface cover (Figure 7.9) or total volumetric cover (Figure 7.10) (see below). However, the communities growing on both perturbed treatments and controls showed large fluctuations during this period (Plates 7.7 and 7.8). For example, volumetric cover on Treatment 2 (repeat) peaked during February (Figure 710), and both Treatments 2 (repeat) and 4 (repeat) developed lower surface and volumetric covers than the control communities during the early spring (i.e. March; Figures 7.9 and 7.10 respectively).

The percent similarities of algal genera between the control and perturbed treatments also showed a return to levels equivalent to those recorded between the control replicates, whether in terms of generic presence/absence (Figure 7.11), percent surface cover (Figure 7.12), or volumetric cover (Figure 7.13). However, high variability in community composition occurred during this period, due to the large fluctuations in similarity between the perturbed treatments and control replicates.

Rate of re-colonisation

A return to previous levels of community structure prior to perturbation was not used as an estimate of recovery due to possible seasonal effects during the re-colonisation period. Instead, the perturbed community was considered to have recovered when it attained a level of recorded cover equal to the control treatments. Consequently the number of days between the perturbation event and when the recorded parameters first match those of the controls was considered to be an estimate of the recovery time. Hence the recovery time was assessed in terms of the number of genera (Figures 7.14 and 7.8), percent surface cover (Figures 7.15 and 7.9) and volumetric cover (Figures 7.16 and 7.10), for the summer and winter perturbations events respectively.

The recovery time in terms of generic similarity between control and perturbed treatment communities, for presence/absence (Figures 7.17 and 7.11), percent surface cover (Figure 7.18 and 7.12) and

volumetric cover (Figures 7.19 and 7.13) was also determined in a similar way for both the summer and winter perturbations respectively. However one difference was incorporated. Since the control replicates were assumed to have similar algal community structure and composition, the percent similarity between them should have theoretically been constant over time. Therefore a linear regression line was employed to reduce the level of variability recorded between the replicates. Hence recovery time was estimated from when the perturbed treatments attained a level of similarity equal to the regression line of the control replicates. It is important to note that this modified method was not used for the actual measurements of number of genera, surface and volumetric cover described above, as with these data it was not possible to disassociate seasonal variability and variability between the control replicates.

The recovery time or duration of re-colonisation, for the each of the parameters used to describe the perturbed algal communities is shown in Figure 7.20. Overall, the algal communities recovered from perturbation five times more quickly during the winter than in the summer. Furthermore, there appeared to be a decline in recovery time during the summer, towards winter rates, while recovery during the latter season appeared more constant (although only two perturbations events were conducted, compared to four in the summer). Of the different parameters used to describe the algal communities, similarity estimates produced comparatively similar rates of recovery during the different seasons, while the other parameters, based on the direct measurements of community structure, showed wide variation.

7.3.3 Effects of seasonality

Seasonal trends in standing crop (height) of the algal communities were observed for all treatments. For example during summer/autumn, the control treatment (which simulated the natural algal community) supported a low standing crop (Figure 7.21). This trend was emulated by Treatments 1-4 (Figures 7.22, 7.23, 7.24 and 7.25 respectively), even after perturbation, except for Treatment 3 which retained a lower standing crop than the control treatment throughout the remainder of the summer (Figure 7.24). In contrast, the standing crop of the control treatment rapidly increased from January onwards over the winter (Figure 7.21). This trend was also evident in Treatments 2 (repeat) and 4 (repeat) (Figures 7.26 and 7.27 respectively), although the perturbation event appeared to induce a large standing crop as both perturbed communities grew larger than the control treatment, especially Treatment 2 (repeat) during February (Figure 7.26; Plate 7.8).

Seasonal changes in standing crop of the different treatments also correlated with seasonal patterns of generic abundance and re-colonisation of the genera recorded within the algal communities. Similar seasonal trends in the latter were also observed between treatments. For example, during summer, the algal community on the control treatment was dominated by the filamentous genera, *Polysiphonia*, *Herposiphonia*, *Sphacelaria* and to lesser extent *Cladophora* and the crustose algae, *?Ulvella* (Figure

7.28). There were also markedly seasonal appearances by microalgae and unidentified juvenile phaeophytes (probably *Padina* and/or *Sargassum*). However, by autumn and early winter, there was an increased abundance of Rhodophyta, such as *Ceramium*, *Centroceras* and *Crouania*, as well as an increased dominance by *Polysiphonia*. Chlorophyta became less prominent by winter, being restricted to the earlier summer months. Similar patterns of generic abundance were observed for Treatments 1-4 (Figures 7.29, 7.30, 7.31 and 7.32 respectively). After perturbation the algal communities of Treatments 1-4 were all characterised by the rapid re-colonisation of *Herposiphonia*, also with *Polysiphonia* at the beginning and end of the summer/early autumn period (Table 7.4). However, due to the marked seasonality of microalgae during the middle of this period, the cyanophyte assemblage subsequently became a dominant initial colonist, along with *Herposiphonia* and the crustose algae, *?Ulvella*, for Treatment 3 (Plate 7.3).

During winter, the control treatment community was characterised by a reduced generic diversity, dominated by *Polysiphonia* and *Sphacelaria* and to a lesser extent, *Herposiphonia* and *Cladophora* (Figure 7.33). Of particular significance was the marked seasonal appearance and brief dominance by *Feldmannia/Hincksia* during February (Plates 7.7 and 7.8). Similar patterns of generic abundance were observed for the perturbed treatments (Figures 7.34 and 7.35 respectively). For example, after perturbation, the algal communities of Treatments 2 (repeat) and 4 (repeat) were quickly re-colonised and dominated by *Polysiphonia* and *Sphacelaria* (Table 7.4). There was also brief dominance by *Feldmannia/Hincksia*. Treatment 2 (repeat), in particular, developed an abundance of *Feldmannia/Hincksia* that was almost twice as large as that recorded for the control treatment (Plate 7.8). A further divergence from the control treatment, that developed after perturbation, was the increased dominance of *Enteromorpha* and *Cladophora*. However, this may have been in response to a further perturbation event due to abrasive action of macroalgal stands (i.e. *Sargassum*) adjacent to the settlement panel (Plate 7.9).

7.4 Discussion

7.4.1 Experimental design

The composition of the perturbed and unperturbed benthic algal communities at Abu Ali exhibited wide spatial and temporal variation, as revealed by the differences in generic and total volumetric cover between the treatments (Plates 7.3 and 7.8). An example is the differences that developed between the two control replicates throughout the study period, especially in terms of percent similarity. (Although in this case, it is important to note that the differences were only in algal cover as community composition (number of genera) was not significantly different between replicate settlement plates). The variability or divergence observed between replicate and treatment was more prevalent during winter, and due to the dramatic increase in algal cover and increased dominance by one or two seasonally active genera (i.e. *Feldmannia/Hincksia*; Plates 7.1 and 7.2). This potentially high level of

variability meant that the individual results of the perturbation treatments were susceptible to bias, especially considering their lack of replication. Unfortunately, logistical and financial constraints prevented the deployment of replicate treatment panels. However, although seasonality strongly influenced the number of genera and volumetric cover, the total surface cover across the settlement plates remained relatively constant.

A key feature of the experimental design is that the sampling procedure was temporally independent, thus permitting statistical analyses of the effects of time. Many previous studies have investigated the process of succession by repeatedly re-examining the community composition of the same experimental plots (Sousa, 1979a,b; Farrell, 1989, 1991; McCook and Chapman, 1991, 1993), or artificial settlement plates (Sutherland and Karlson, 1977; Breitburg, 1985; Turner and Todd, 1993) through time. Consequently, effective isolation and analysis of temporal effects were not possible in these studies. Underwood and Anderson (1994) have advocated the use of methodology incorporating independent temporal sampling. As demonstrated in this study, settlement plates can be established *in situ* simultaneously and then sampled only once throughout the study period.

7.4.2 Seasonal patterns and rates of succession

The results clearly indicate that after perturbation the algal communities returned to their natural state (i.e. a community dominated by filamentous algal forms), although the actual recovery time was dependent on season and the parameters measured. Furthermore, the order of re-colonisation was strongly influenced by the seasonality of life-histories of individual genera. For example, *Herposiphonia*, *Polysiphonia* and microalgae predominated in summer, and *Polysiphonia*, *Sphacelaria* and *Feldmannia/Hincksia* in winter.

The rate of re-colonisation was also influenced by the seasonal dominance of particular genera (i.e. algal cover, and generic composition recovered approximately five times faster in winter than in summer). However, it is important to note that the control treatments supported a lower generic diversity in winter, due to the increased dominance of several genera (notably *Sphacelaria* and *Feldmannia/Hincksia*). Therefore the perturbed communities were not required to develop as high a community diversity as in the summer in order to be considered as having recovered, which was consequently more quickly attained. The winter proliferation of dominant genera also resulted in quick recovery of volumetric cover and similarities with the algal communities on the control treatments. In contrast, the higher generic diversity of algal communities in summer, and therefore potentially competitive successional interactions, resulted in a longer period of re-colonisation and community development after perturbation. The apparent decline in recovery rate for the communities perturbed during the summer and early autumn period may also reflect a seasonally decreasing generic diversity at this time (i.e. the disappearance of microalgae towards winter).

It is important to note that the rapid seasonal growth recorded in winter, although apparent on the control replicates, was far more pronounced on the perturbed treatments (Plate 7.8). Hence the seasonal colonisation and growth of algae on the control replicates was being inhibited; either by abiotic factors (i.e. sediment covering available substratum) or biotic factors (i.e. algae already occupying colonising space). The perturbation event temporarily removed both of these constraints to settlement by exposing the substratum, and the treatment plates were rapidly colonised. During summer, sediment levels on the settlement plates were low, probably due to the abrasive activities of grazing herbivores (Plates 7.3, 7.4 and 7.5) and seasonal environmental conditions (Chapter 4). In winter, sedimentation increased (Plate 7.6), probably due to environmental conditions (Chapter 4) and a decline in herbivore activity (Chapter 8). However, the settlement plates may have been biased towards entrapping higher levels of sediment due to their flat, uniform topography (see Chapter 5). Therefore, in addition to seasonally increased sedimentation rates (see Chapter 4), the level of inhibition of algal settlement from sedimentation during winter may have been artificially enhanced compared to events on the natural substratum (Plate 7.2).

Overall the pattern and rate of succession in the benthic algal communities were dependent on the time of year in which the community was perturbed. Other studies have also shown the importance of season in the patterns of recruitment and succession of sessile marine assemblages (Sutherland and Karlson, 1977; Osman, 1978; Keough, 1983; Farrell, 1991; Turner and Todd, 1993). However seasonal patterns of succession can produce different assemblages and, depending on the stability of the resultant community, alter the characteristics and quality of the benthic community. For example, the sessile marine assemblage manipulated by Underwood and Anderson (1994) developed multiple stable states (*sensu* Sutherland, 1974), either oyster-, algal- or barnacle-dominated, depending on the time of year the successional process was initiated.

In the present study, while perturbations throughout different seasons produced variable patterns and rates of succession, the different communities established were not stable over the entire study period (i.e. the life-spans of the temporarily dominant algae were too short). Hence, the algal community was never permanently dominated by one particular genus, but instead always comprised an assemblage of filamentous algae that, despite seasonal variations, had a fairly predictable composition for any given time of year.

Treatment	Perturbation time scale	
	Summer	**Winter**
1	t = 0 weeks (14/8/94)	
2	t = 2 weeks (25/8/94)	t = 0 weeks (8/1/94)
3	t = 4 weeks (11/9/94)	
4	t = 8 weeks (8/10/94)	t = 4 weeks (1/2/94)

Treatment	Perturbation time scale
Control	
T 1	↑
T 2	↑
T 2 (repeat)	↑
T 3	↑
T 4	↑
T 4 (repeat)	↑
	Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr.

Table 7.1: **Perturbation time scale** and schematic ('↑' indicates perturbation event) for all treatments during the summer and winter, where the first incident of perturbation, in either season, is equal to time zero (i.e., t = 0).

	Control replicates (1/8/94 - 13/4/95)			All treatments (1/8/94 - 14/8/94)		
	ANOVA (2-way without replication)			ANOVA (2-way without replication)		
	n	Treatment	Time	*n*	Treatment	Time
Average number of genera	128	NS $p > 0.1$	S $p < 0.001$	20	NS $p > 0.1$	NS $p > 0.05$
Total percent surface cover	128	S $p < 0.01$	NS $p > 0.05$	20	S $p < 0.01$	NS $p > 0.05$
Index of volumetric cover	128	S $p < 0.05$	S $p < 0.01$	20	S $p < 0.05$	NS $p > 0.1$
Percent similarity (pres./abs.)	128	n/a	n/a	20	NS $p > 0.5$	S $p < 0.001$
Percent similarity (surface cover)	128	n/a	n/a	20	NS $p > 0.5$	NS $p > 0.05$
Percent similarity (vol. cover)	128	n/a	n/a	20	NS $p > 0.5$	S $p < 0.05$

Table 7.2: **ANOVA** results in terms of the number of genera, total percent surface cover, index of volumetric cover and percent similarity for the algal community on the control replicates and on all the treatments two weeks prior to perturbation. Note all data were logarithmically transformed (i.e. $\log(x+1)$). S = significant, NS = non-significant.

	Comparison of Means ($t_{(0.05,3)} = 3.183$)				
	n	**Control vs. Treat. 1**	**Control vs. Treat. 2**	**Control vs. Treat. 3**	**Control vs. Treat. 4**
Percent surface cover	4	S $t = 3.414$	NS $t = 1.406$	NS $t = 1.004$	NS $t = 1.807$
Index of volumetric cover	4	NS $t = 1.005$	NS $t = 0.011$	NS $t = 0.029$	NS $t = 0.003$

Table 7.3: **Comparison of means** (*t*-test) for total percent surface cover and volumetric cover for the algal community growing on the control replicates and all other perturbation treatments during the first two weeks prior to perturbation. S = significant, NS = non-significant.

Season and Treatment		**Sequence of algal generic re-colonisation** (initial six or seven genera)
Summer	**1**	*Herposiphonia*, *Polysiphonia*, *Sphacelaria*, *Bryopsis* and *?Ulvella*, followed by *Cladophora* and microalgae
	2	*Herposiphonia* and microalgae, followed by *Polysiphonia*, *Sphacelaria*, *Ceramium* and *?Ulvella*
	3	*Herposiphonia*, microalgae, *Sphacelaria* and *?Ulvella*, followed by *Polysiphonia* and *Bryopsis*
	4	*Herposiphonia*, *Polysiphonia* and *Ceramium*, followed by *Centroceras*, microalgae and *Crouania*
Winter	**2R**	*Polysiphonia* and *Sphacelaria*, followed *Chaetomorpha*, *Feldmannia/Hincksia*, *Herposiphonia* and *Enteromorpha*
	4R	*Polysiphonia*, *Cladophora*, *Herposiphonia* and *Sphacelaria*, followed by *Feldmannia/Hincksia* and *Enteromorpha*

Table 7.4: **Sequence of algal generic re-colonisation** for all treatments after perturbation during both summer and winter. Initial colonists are given first, followed by successive genera, up to the first six or seven genera to re-colonise the exposed settlement plate surface.

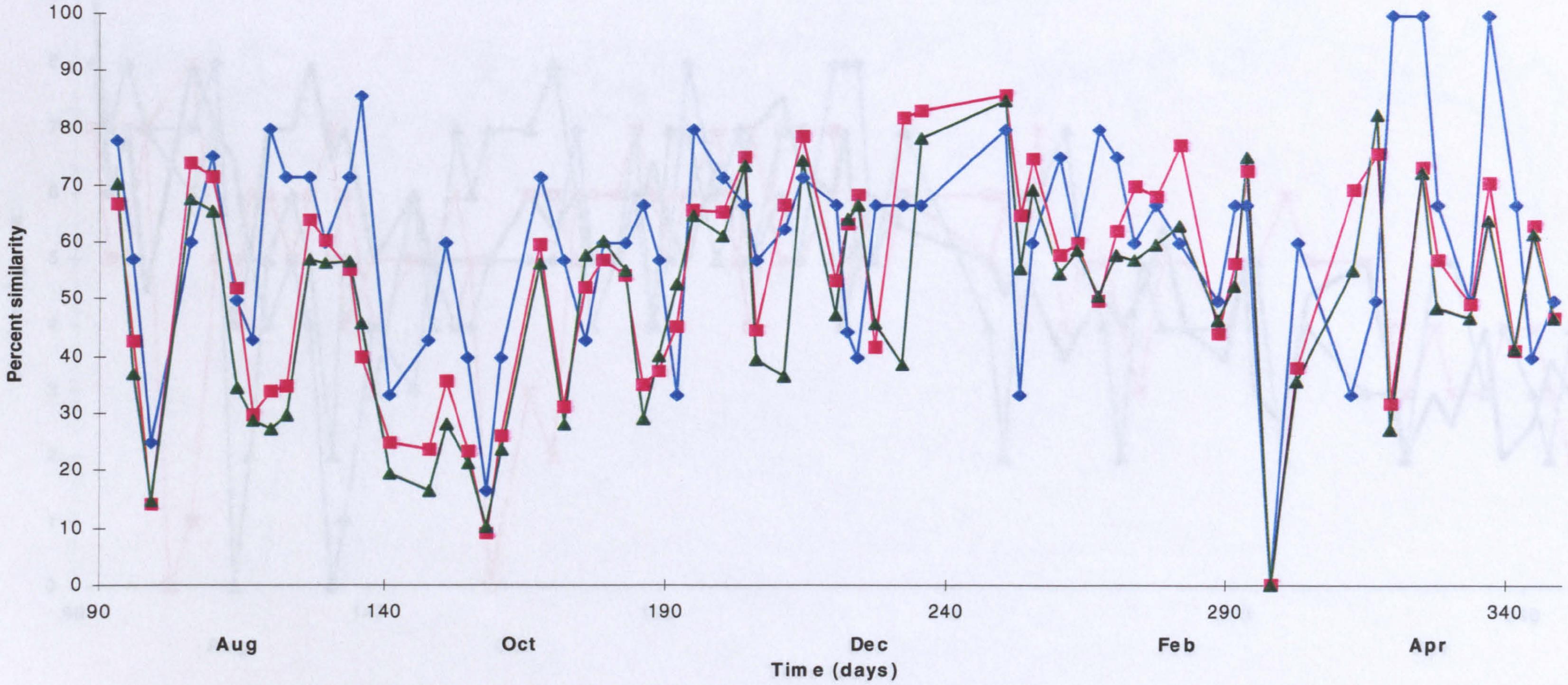


Figure 7.1: The **percent similarity** in generic composition of the algal community between **control replicates** for the entire study period; (◆) presence/absence, (■) surface cover, (▲) volumetric cover.

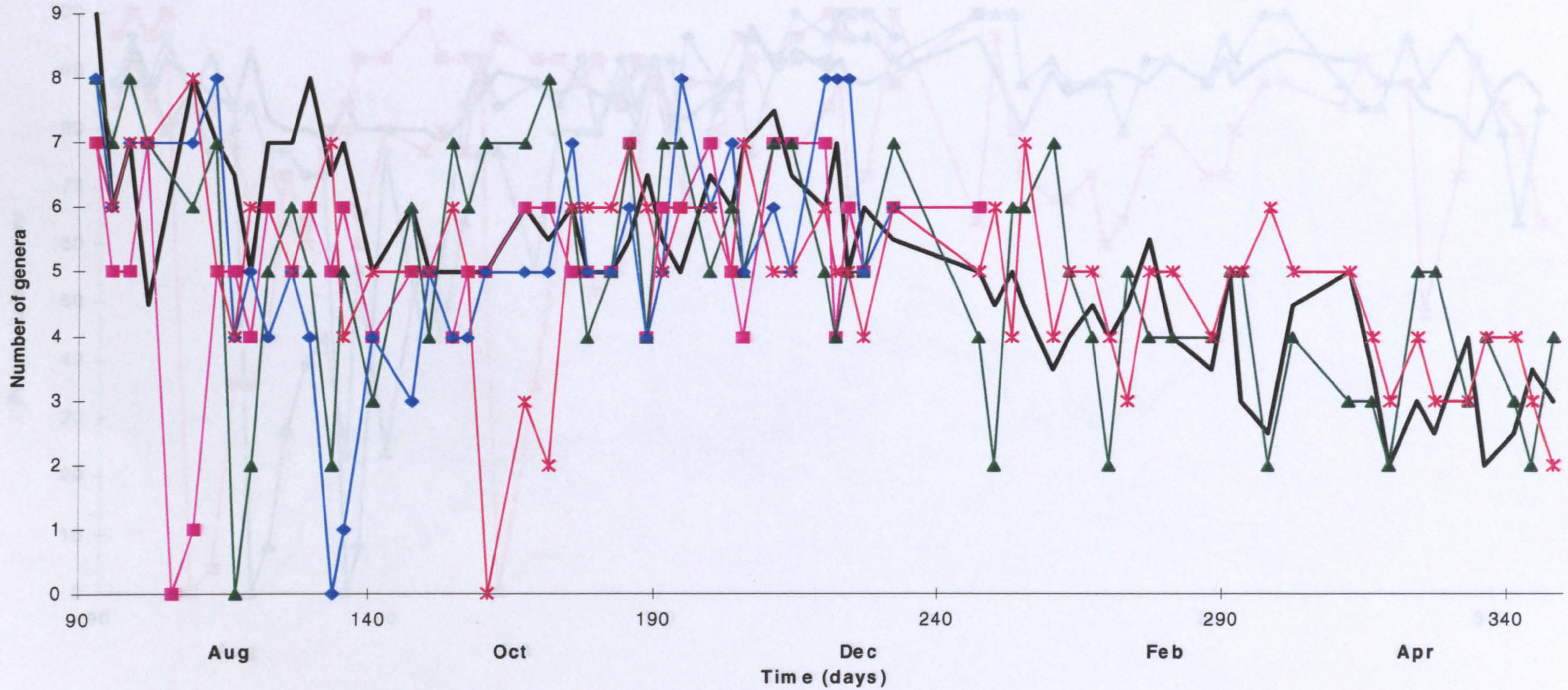


Figure 7.2: The **number of genera** occurring in the algal community growing on **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average number of genera for the control treatment replicates (solid line) is also given.

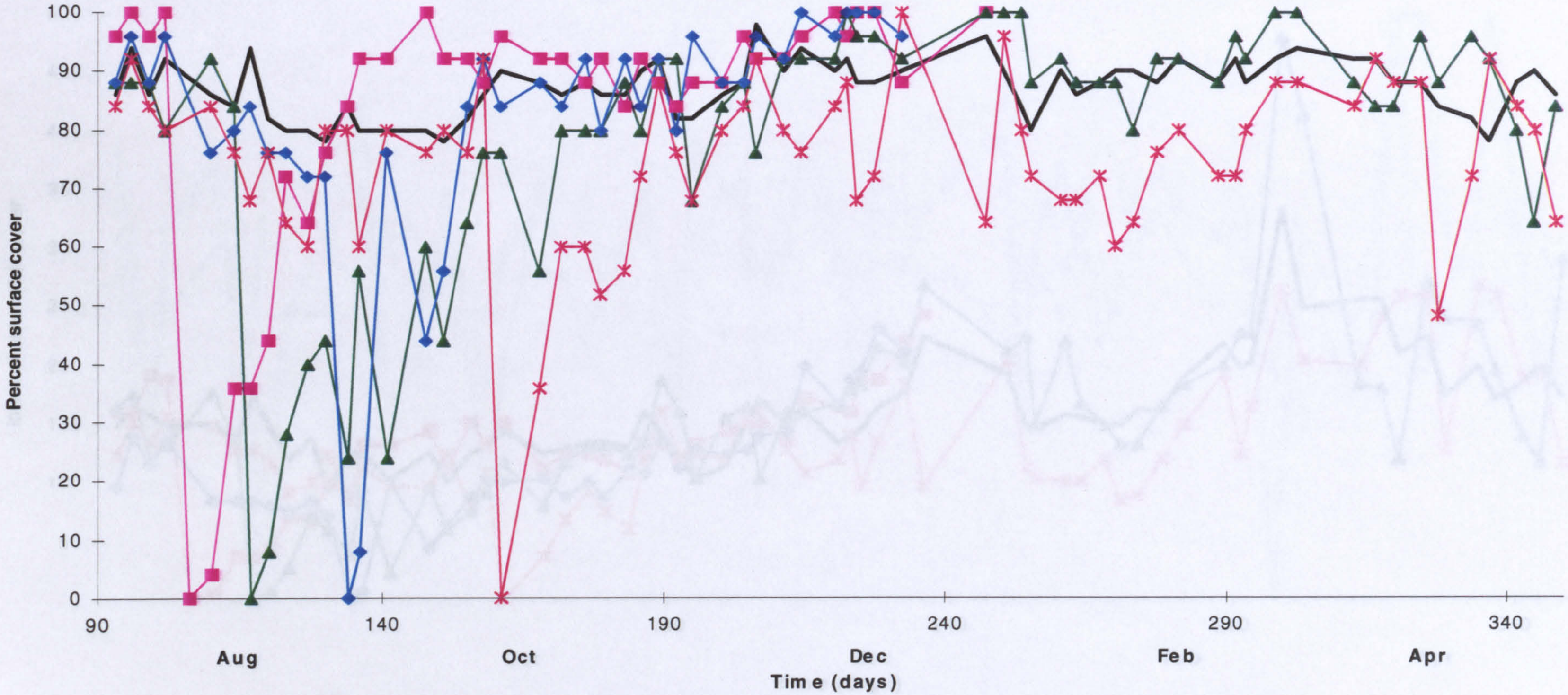


Figure 7.3: The **percent surface cover** of the algal community growing on **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average percent surface cover for the control treatment replicates (solid line) is also given.

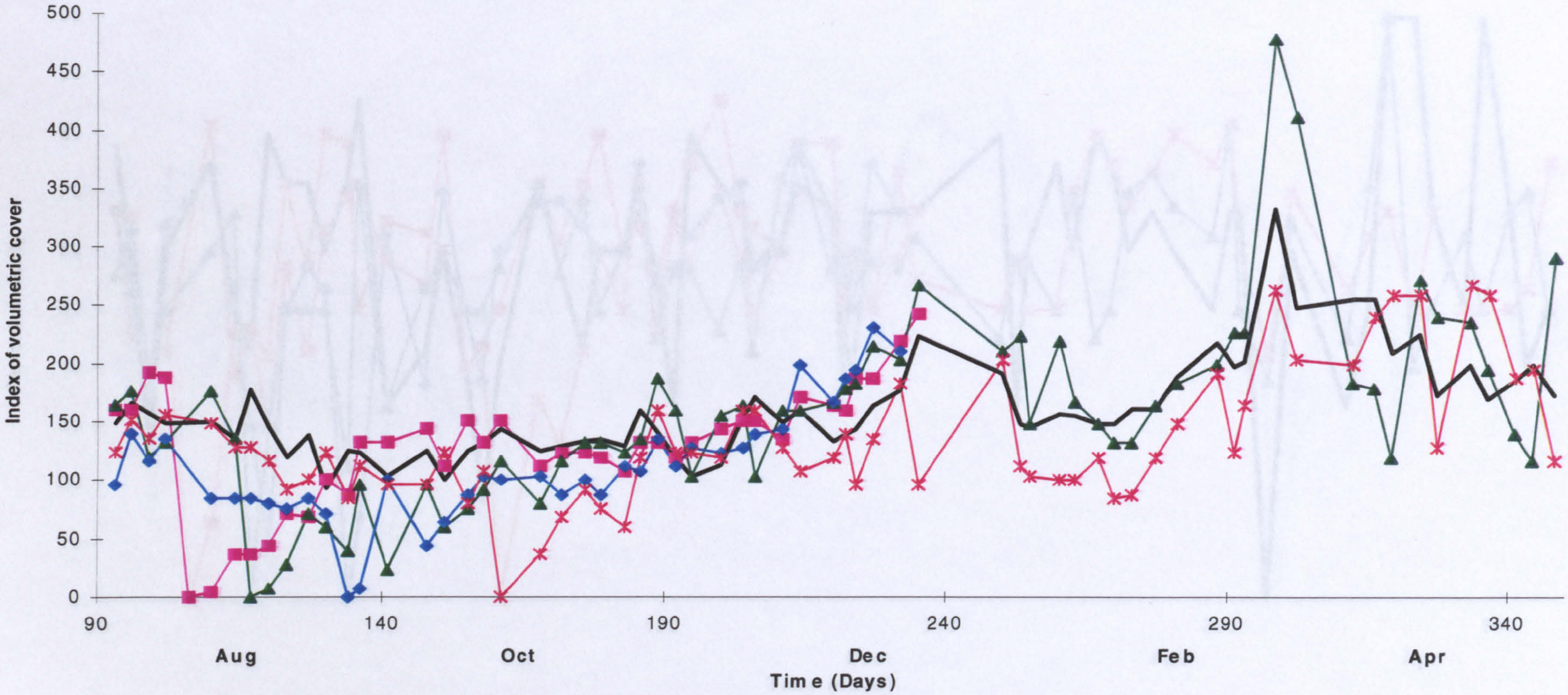


Figure 7.4: The **volumetric cover** of the algal community growing on **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average volumetric cover for the control treatment replicates (solid line) is also given.

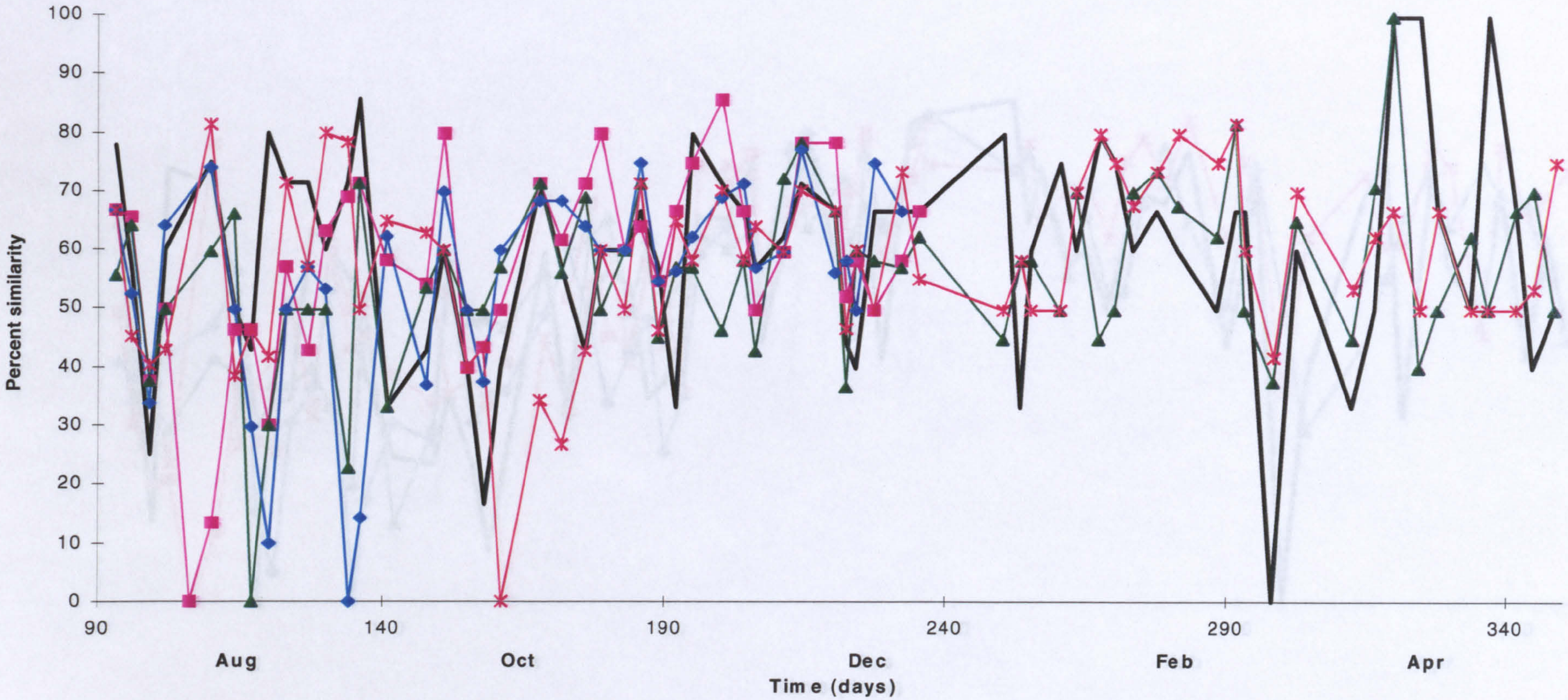


Figure 7.5: The **percent similarity (based on generic presence/absence)** of the algal community between control replicates and **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) is also given.

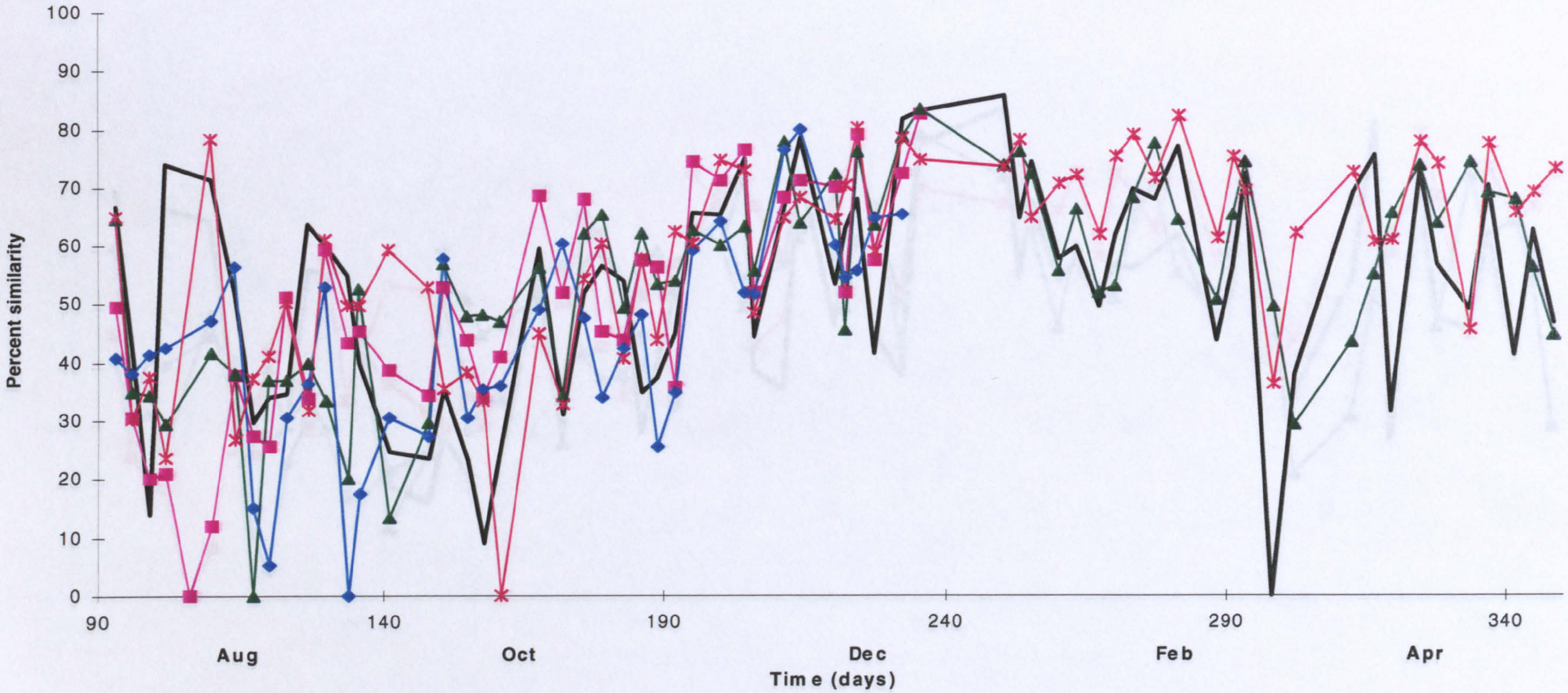


Figure 7.6: The **percent similarity (based on surface cover)** of the algal community between control replicates and **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) is also given.

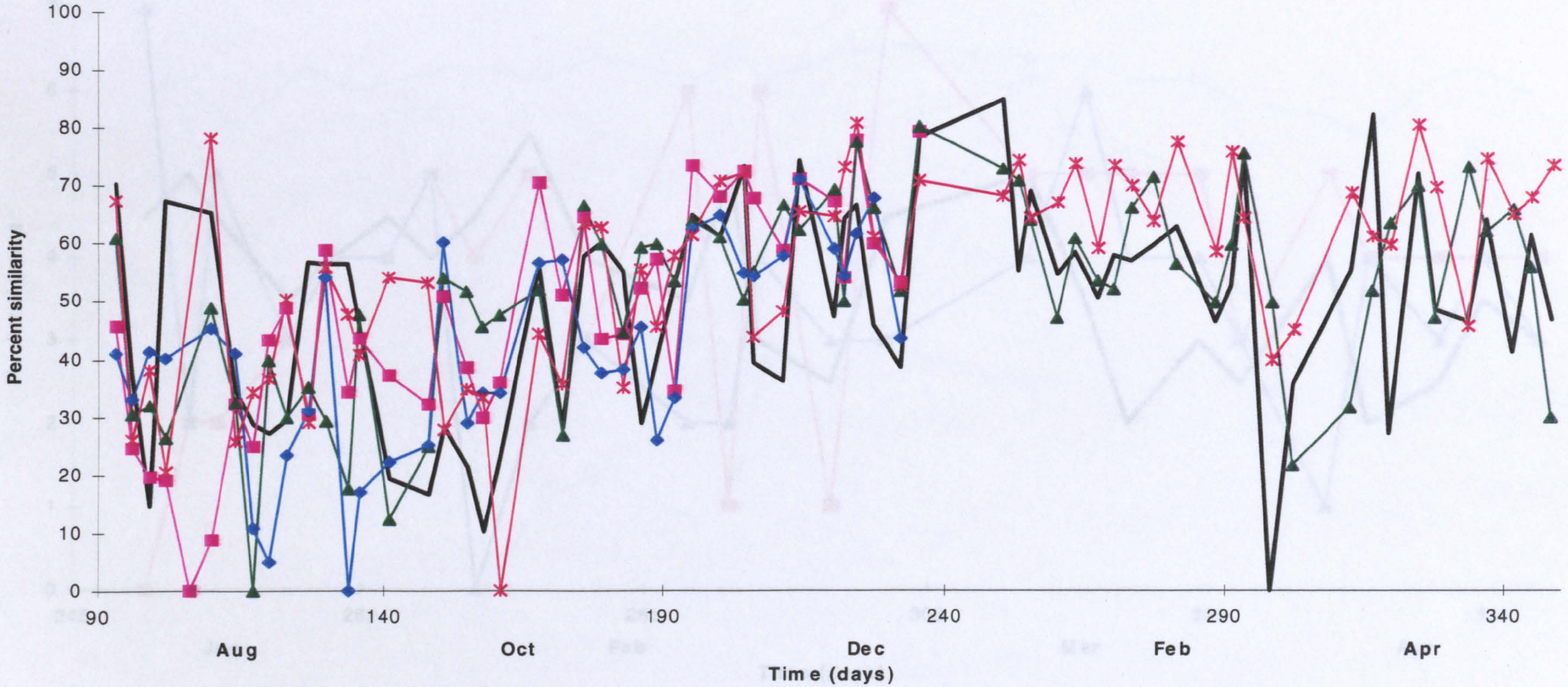


Figure 7.7: The **percent similarity (based on volumetric cover)** of the algal community between control replicates and **Treatments 1-4** before and after perturbation for the entire study period; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) is also given.

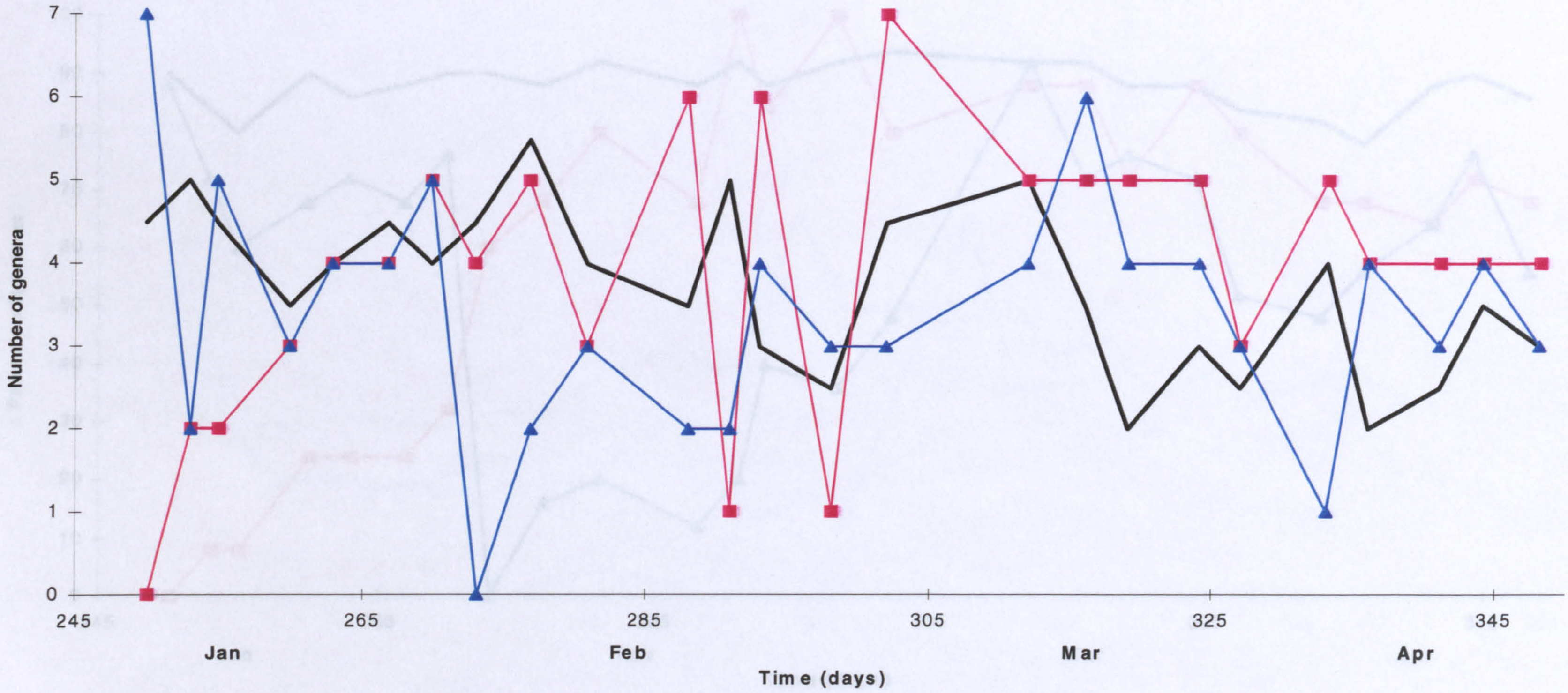


Figure 7.8: The **number of genera** occurring in the algal community growing on **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The average number of genera for the control treatment replicates (solid line) is also given.

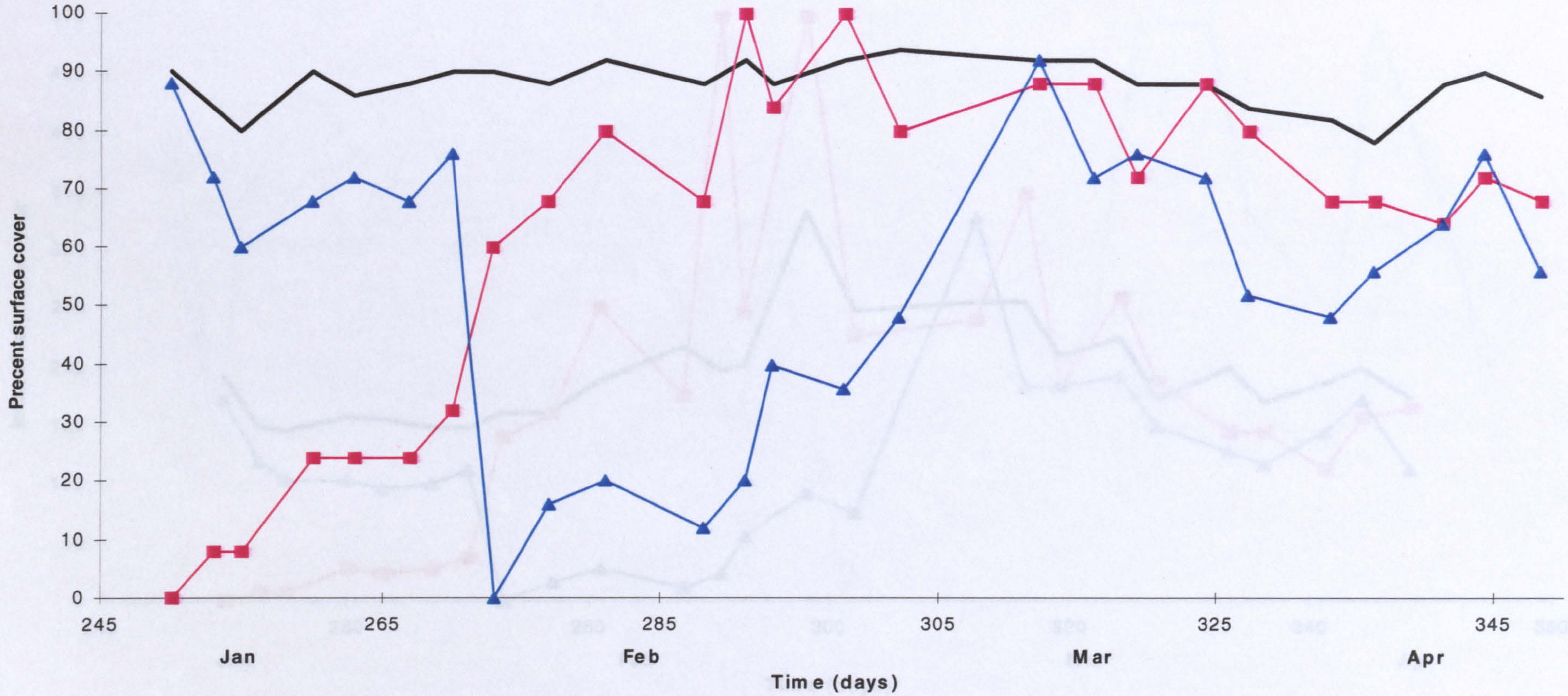


Figure 7.9: The **percent surface cover** of the algal community growing on **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The average percent surface cover for the control treatment replicates (solid line) is also given.

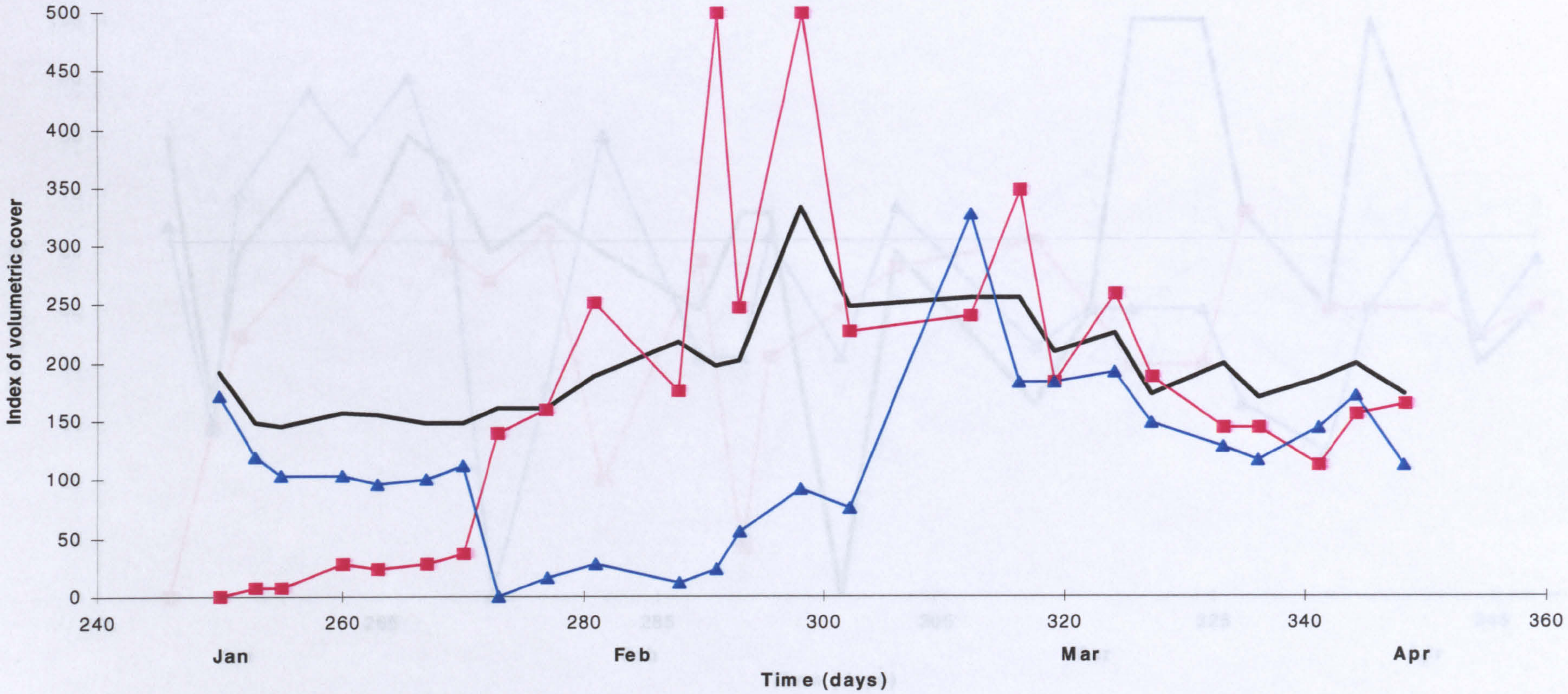


Figure 7.10: The **volumetric cover** of the algal community growing on **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The average volumetric cover for the control treatment replicates (solid line) is also given.

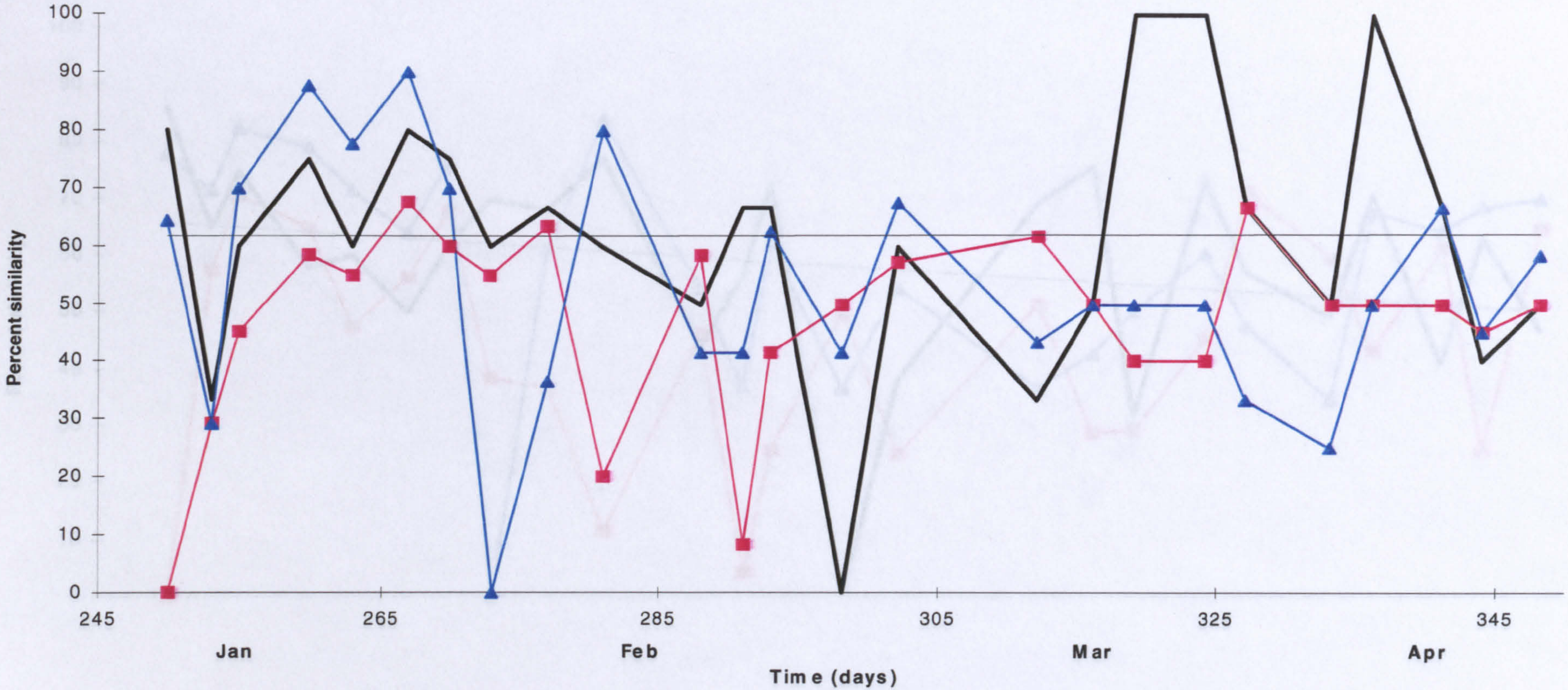


Figure 7.11: The **percent similarity (based on generic presence/absence)** of the algal community growing between control replicates and those from **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

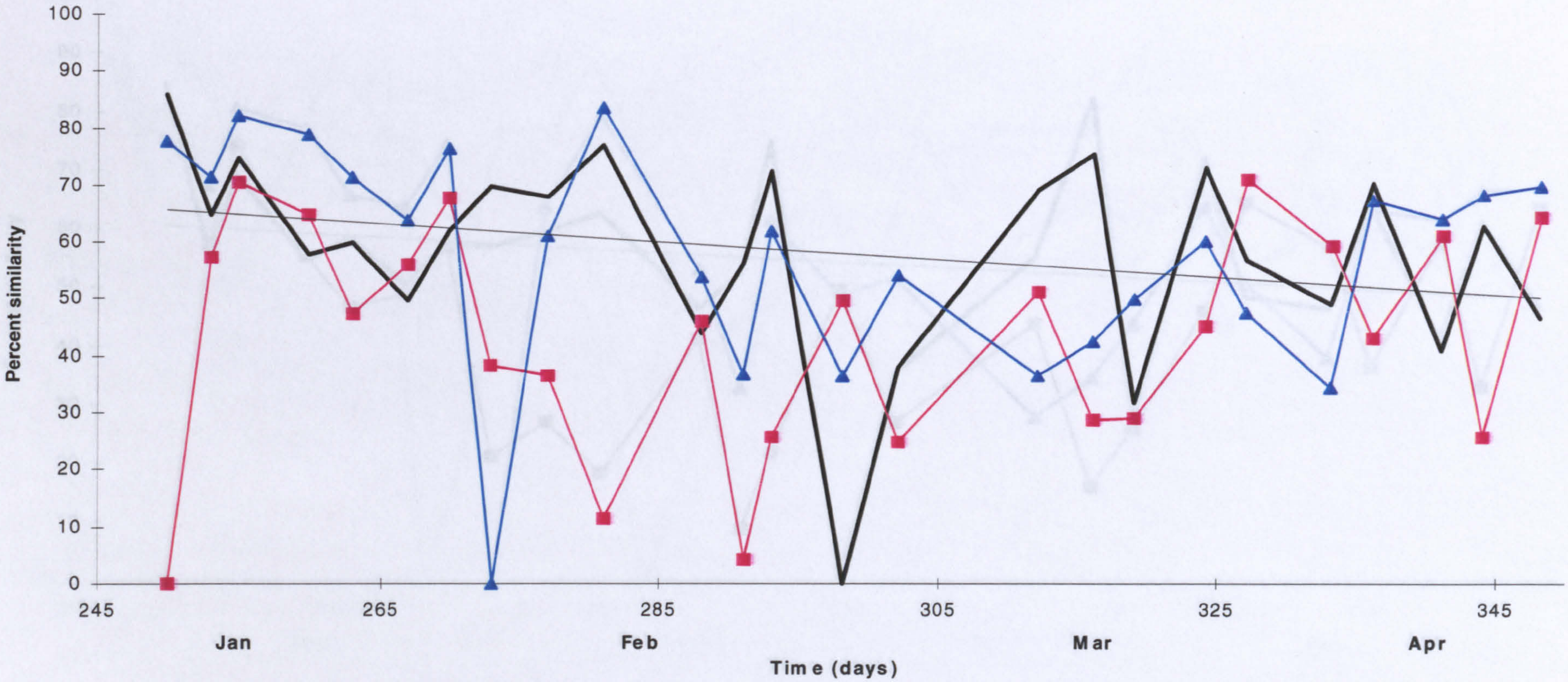


Figure 7.12: The **percent similarity (based on surface cover)** of the algal community growing between control replicates and those from **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

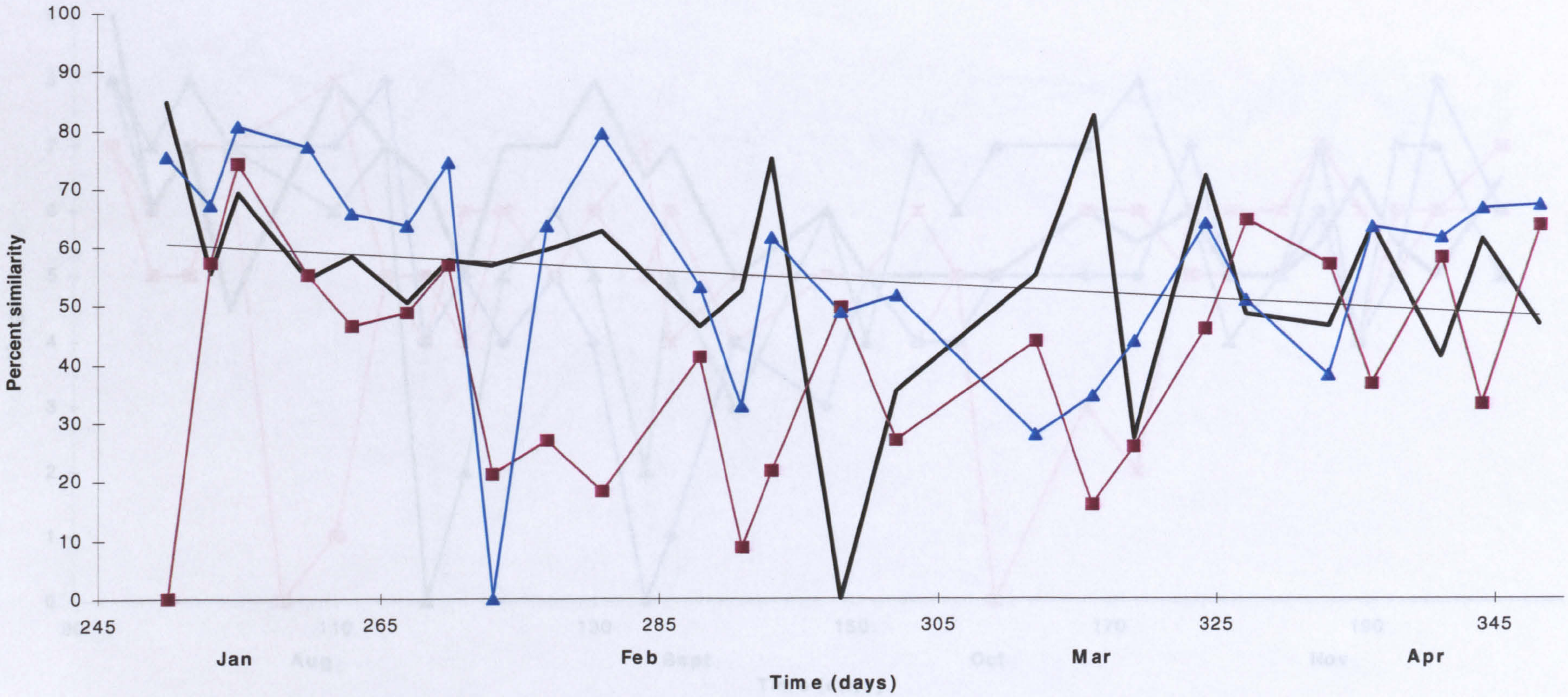


Figure 7.13: The **percent similarity (based on volumetric cover)** of the algal community growing between control replicates and those from **Treatments 2 (repeat) and 4 (repeat)** before and after perturbation throughout the study period; (■) T2R, (▲) T4R. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

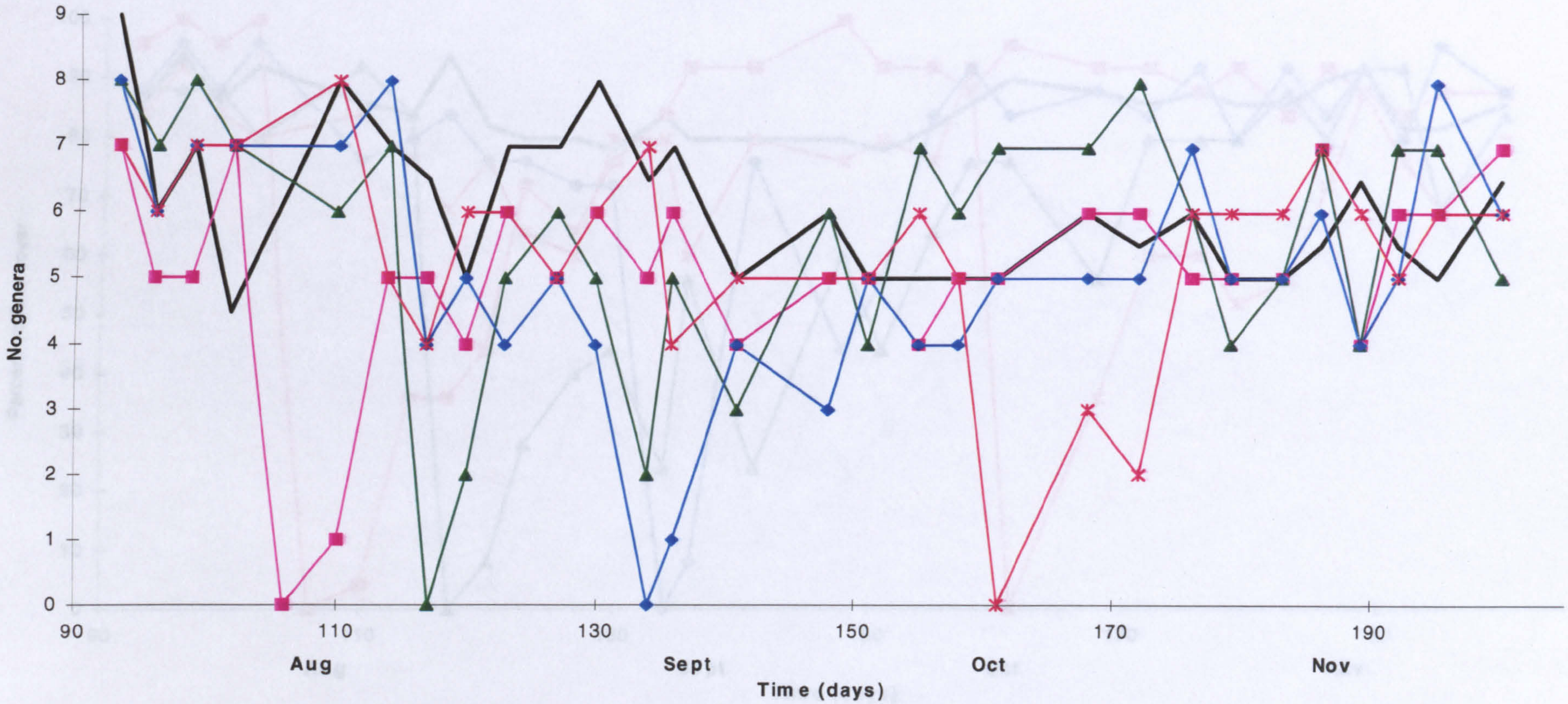


Figure 7.14: The **number of genera** occurring in the algal community growing on **Treatments 1-4** during the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average number of genera for the control treatment replicates (solid line) is also given.

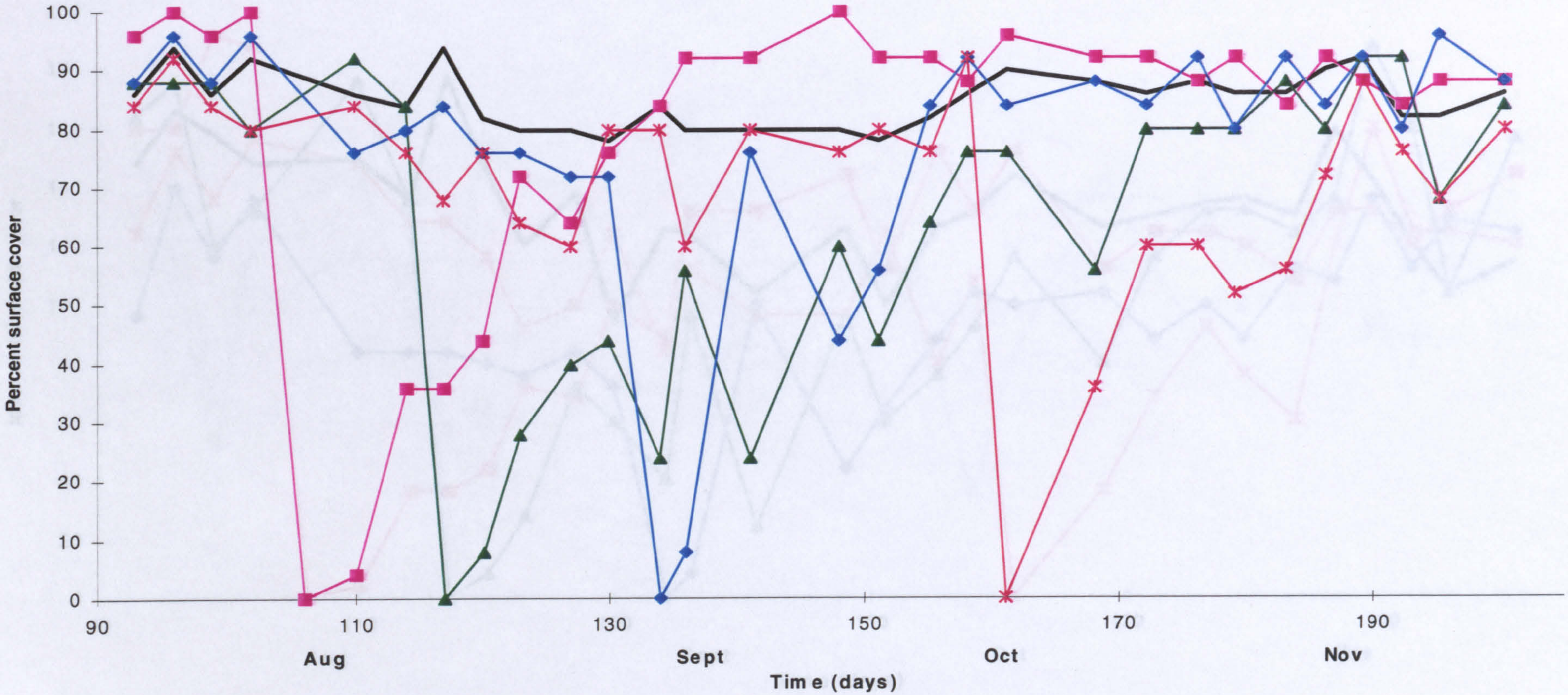


Figure 7.15: The **percent surface cover** of the algal community growing on **Treatments 1-4** during the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average percent surface cover for the control treatment replicates (solid line) is also given.

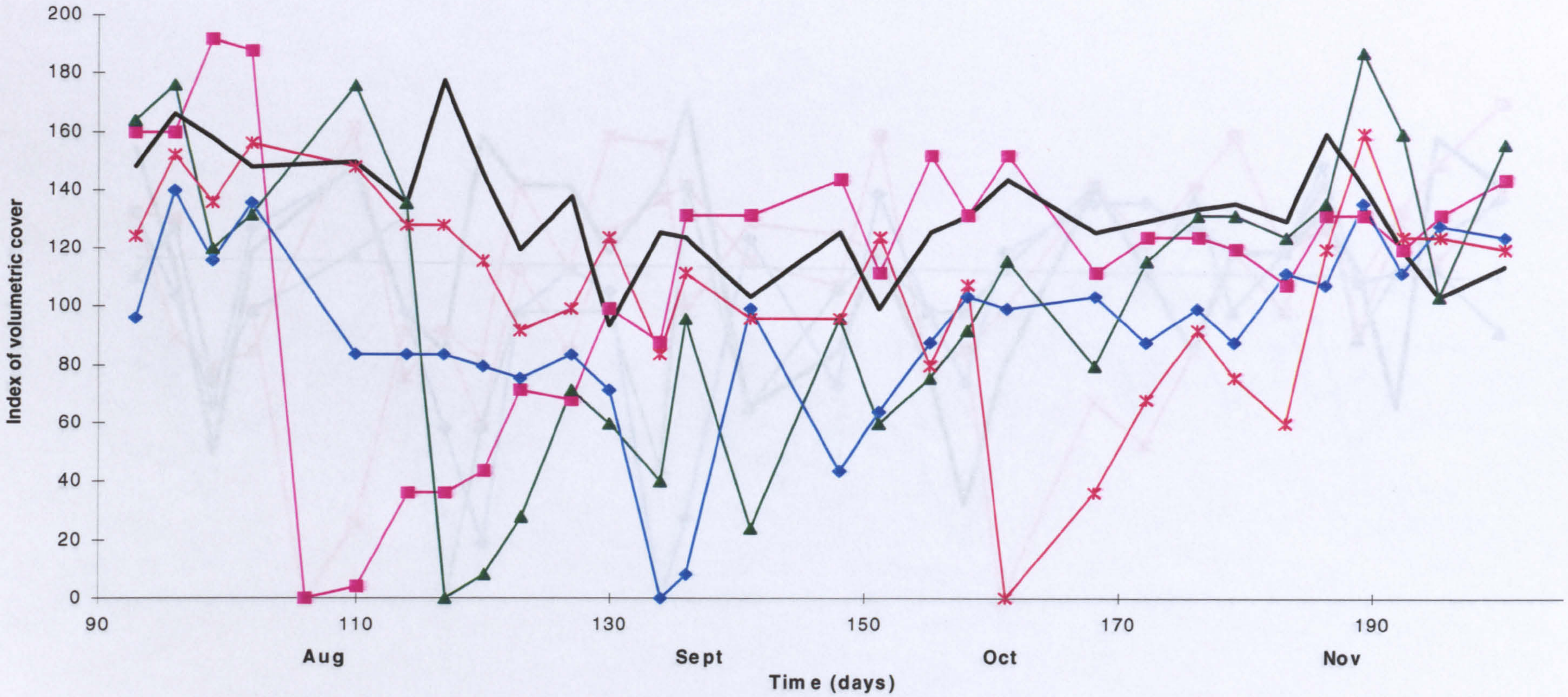


Figure 7.16: The **volumetric cover** of the algal community growing on **Treatments 1-4** during the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The average volumetric cover for the control treatment replicates (solid line) is also given.

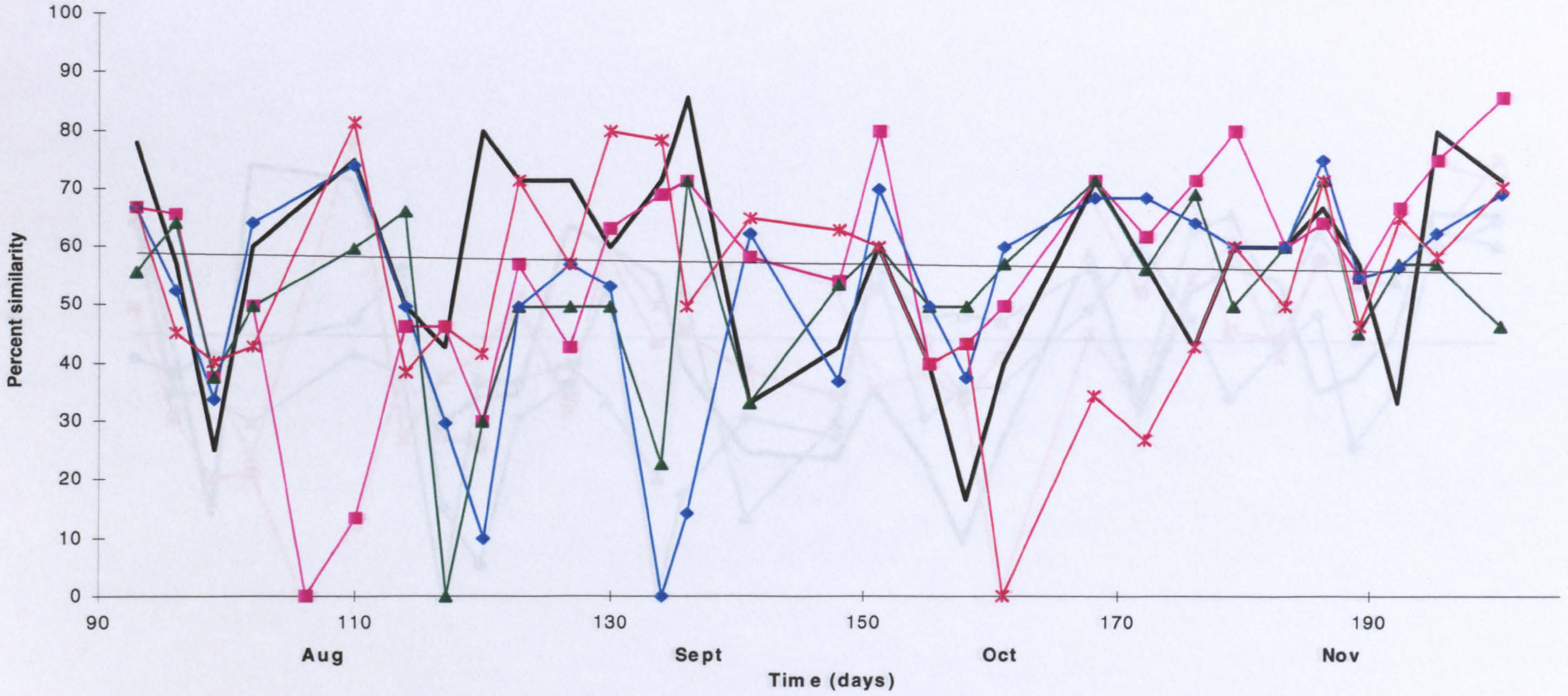


Figure 7.17: The **percent similarity (based on generic presence/absence)** of the algal community between control replicates and **Treatments 1-4** for the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

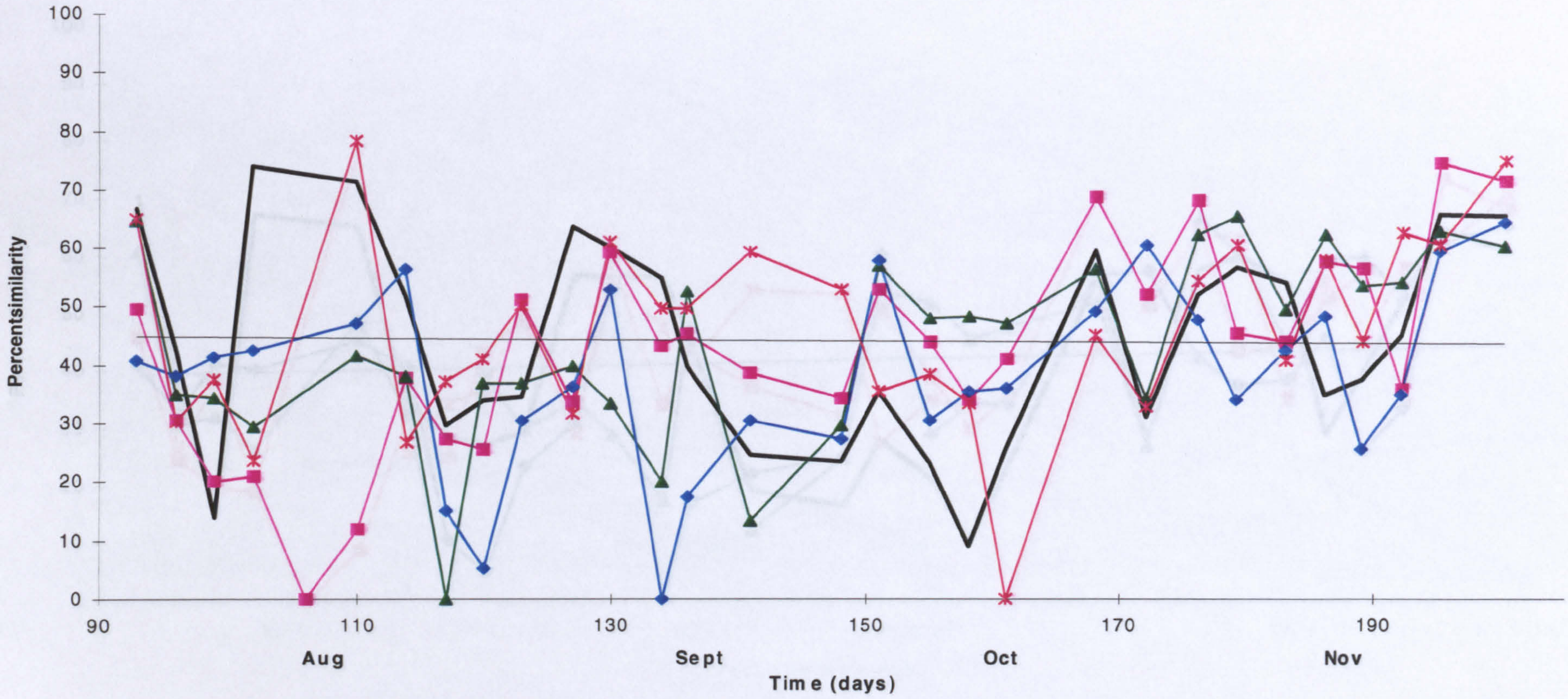


Figure 7.18: The **percent similarity (based on surface cover)** of the algal community between control replicates and **Treatments 1-4** for the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

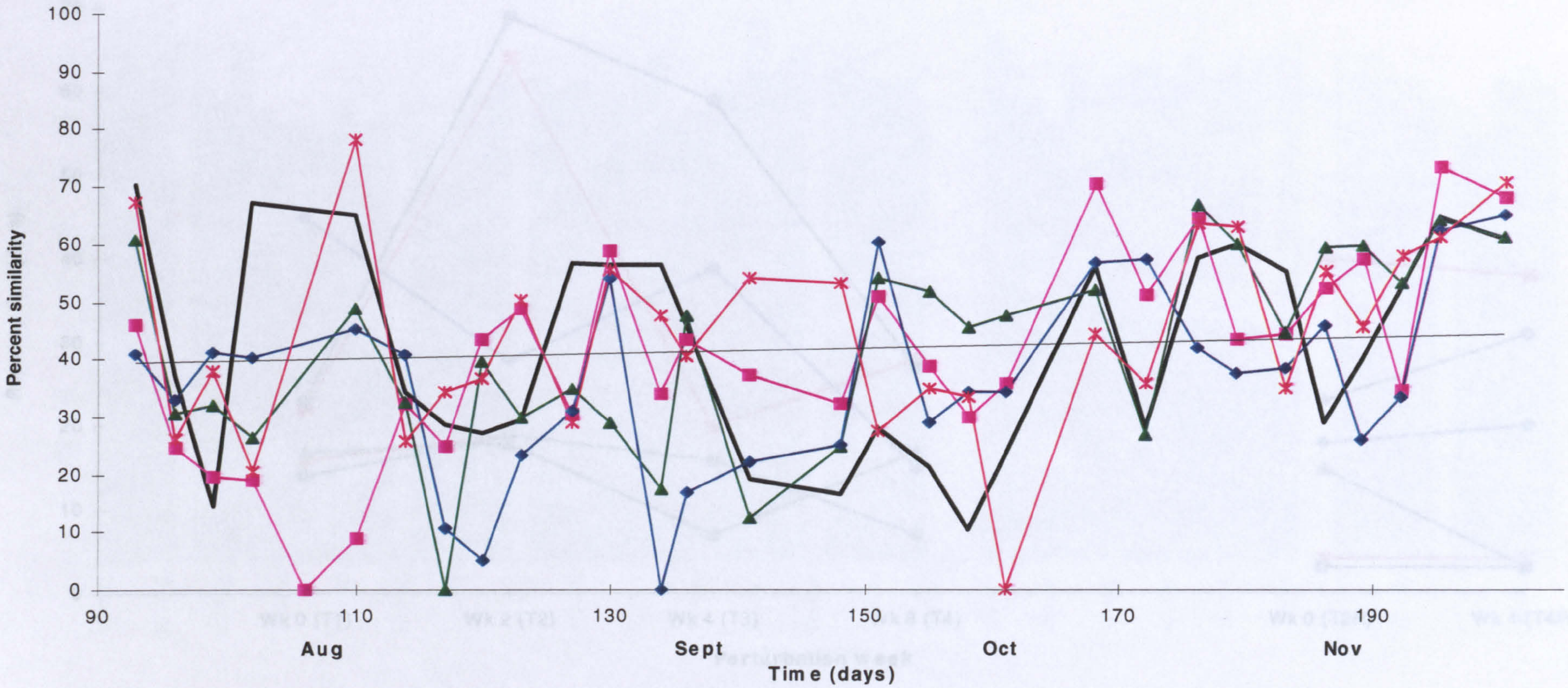


Figure 7.19: The **percent similarity (based on volumetric cover)** of the algal community between control replicates and **Treatments 1-4** for the first **100 days** after the initial perturbation event; (■) T1, (▲) T2, (◆) T3, (✳) T4. The percent similarity between the control treatment replicates (solid line) and its associated linear regression (dotted line) are also given.

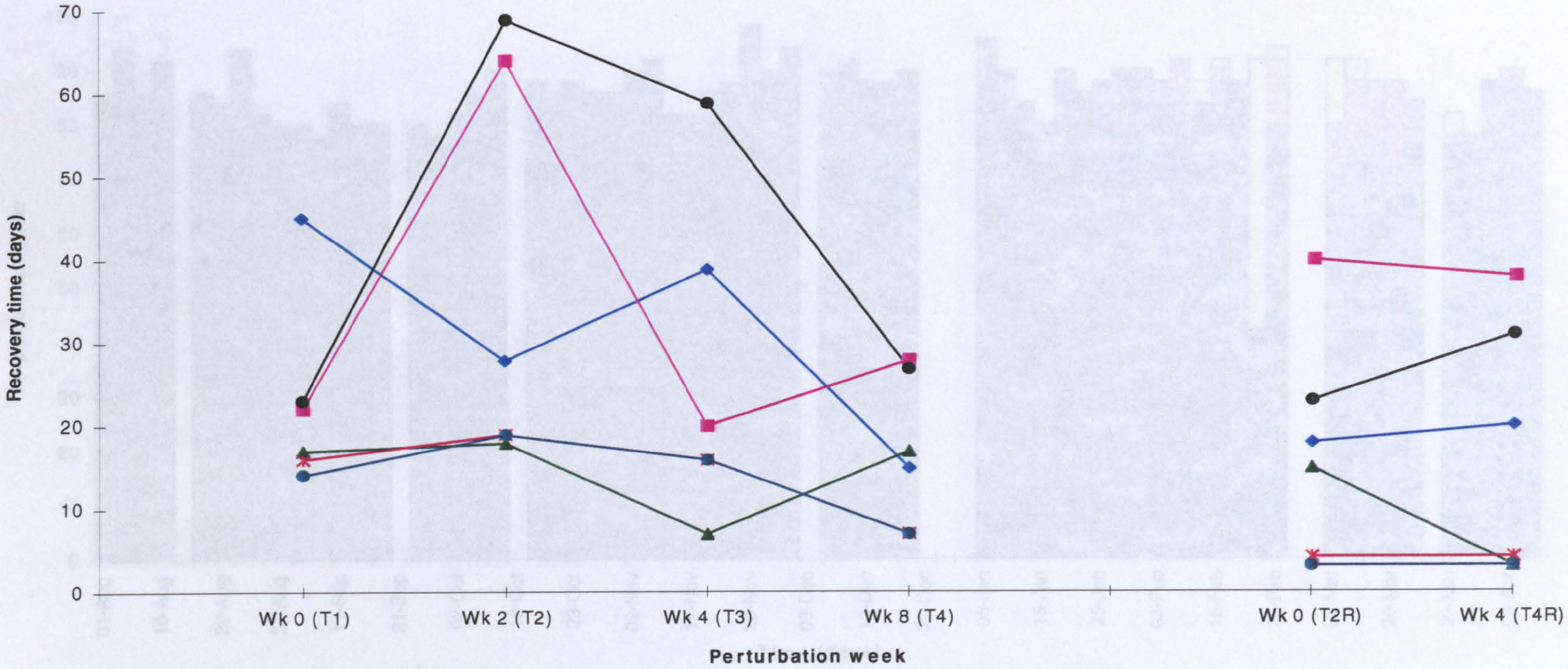


Figure 7.20: The **recovery time** of the algal community after perturbation for **all treatments**; (◆) number of genera, (■) percent surface cover, (●) volumetric cover, (▲) percent similarity (based on generic presence/absence), (✳) percent similarity (based on surface cover), (●) percent similarity (based on volumetric cover).

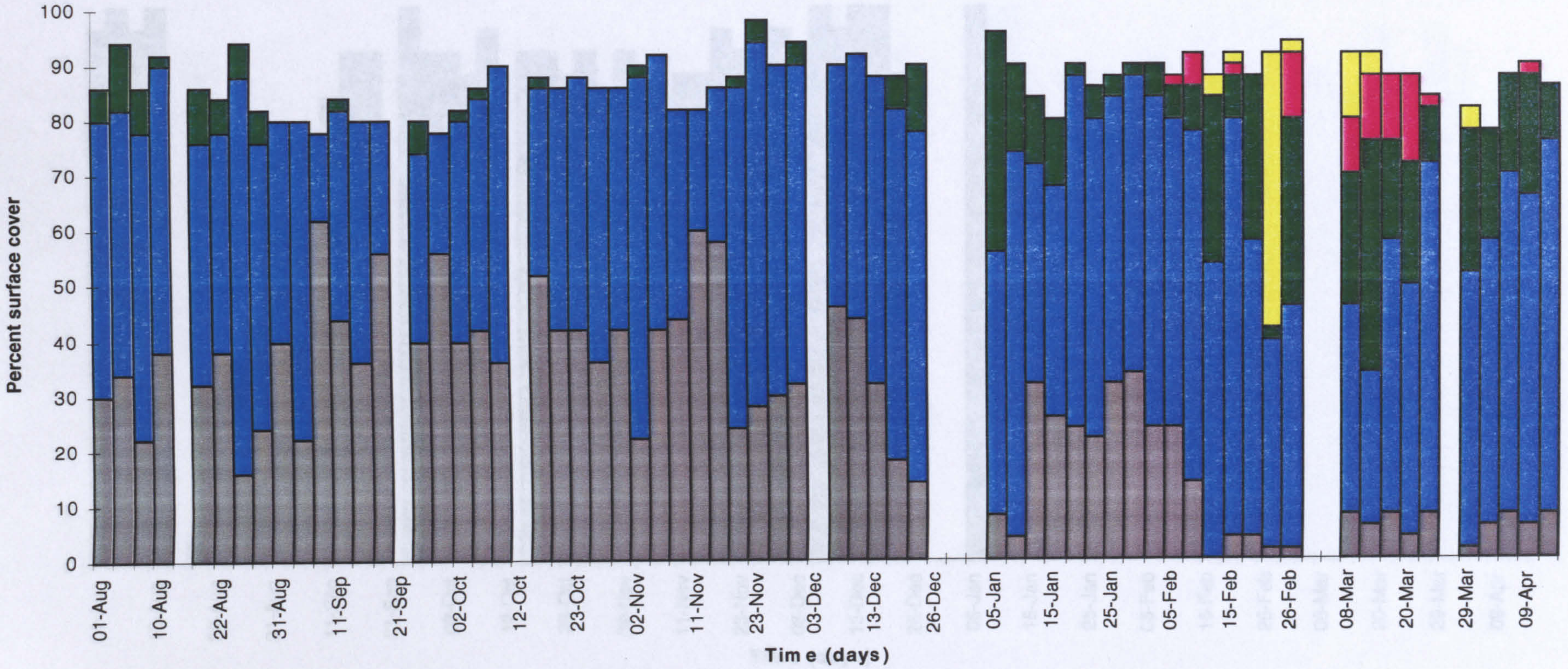


Figure 7.21: Total **percent surface cover** of different **size classes** (SC) of the algal community on the **control treatment** replicates; SC 1 (▪), SC 2 (▪), SC 3 (▪), SC 4 (▪), SC 5 (▪).

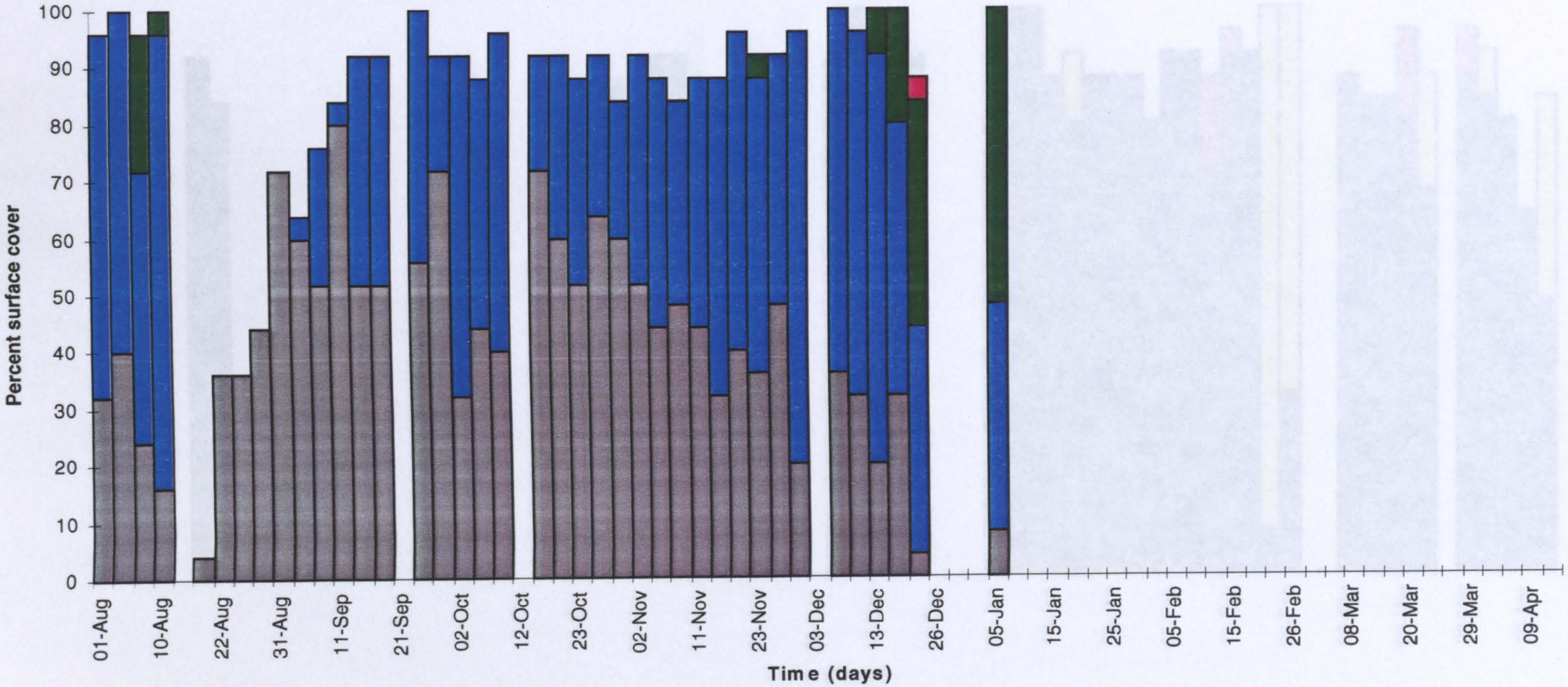


Figure 7.22: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 1**; SC 1 (■), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

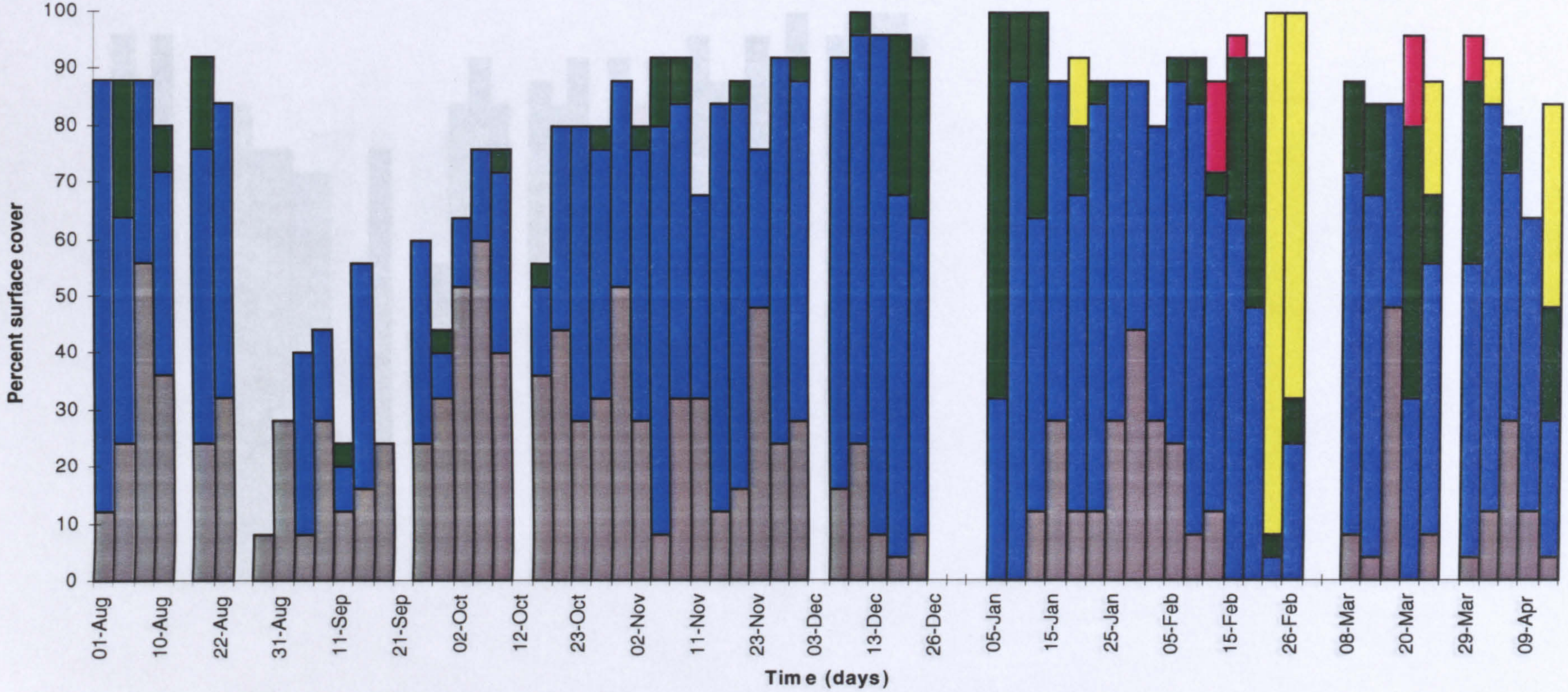


Figure 7.23: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 2**; SC 1 (▒), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

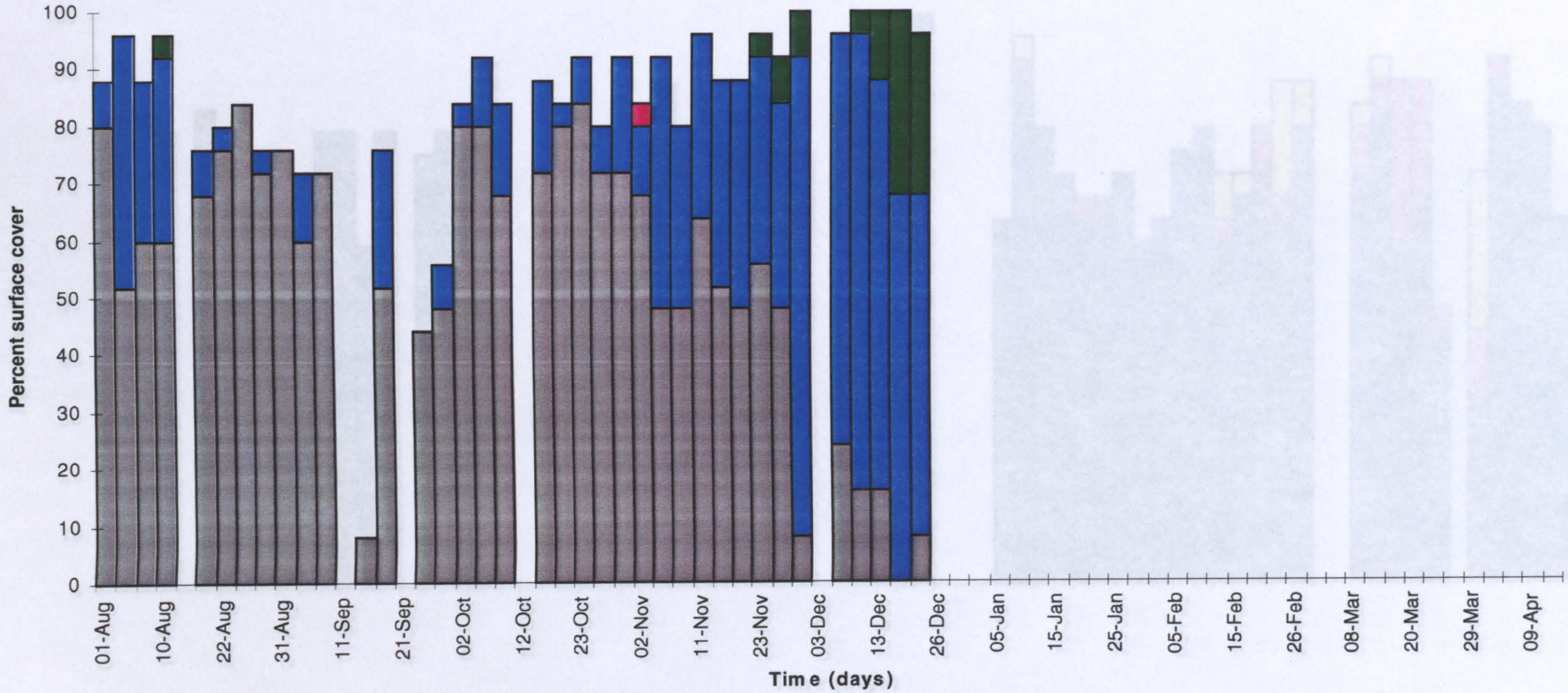


Figure 7.24: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 3**; SC 1 (■), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

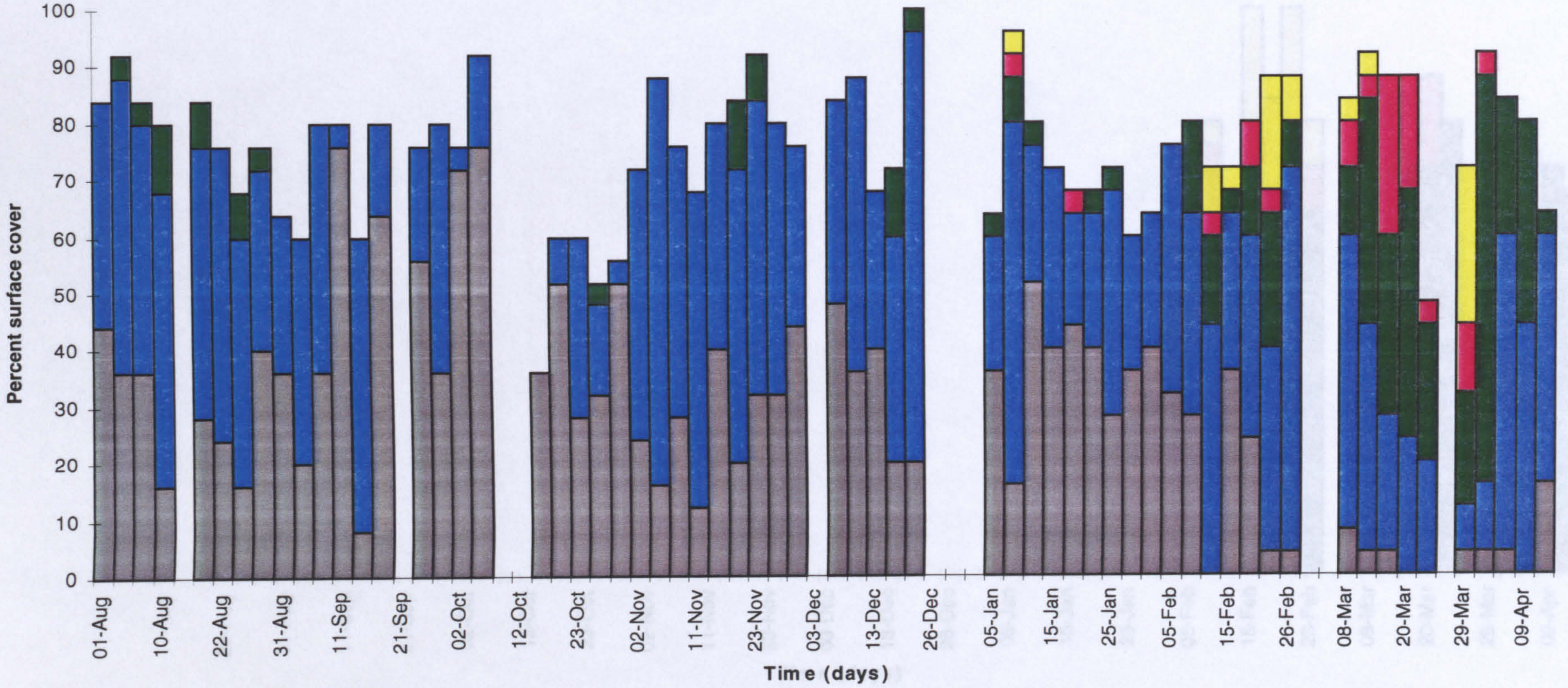


Figure 7.25: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 4**; SC 1 (■), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

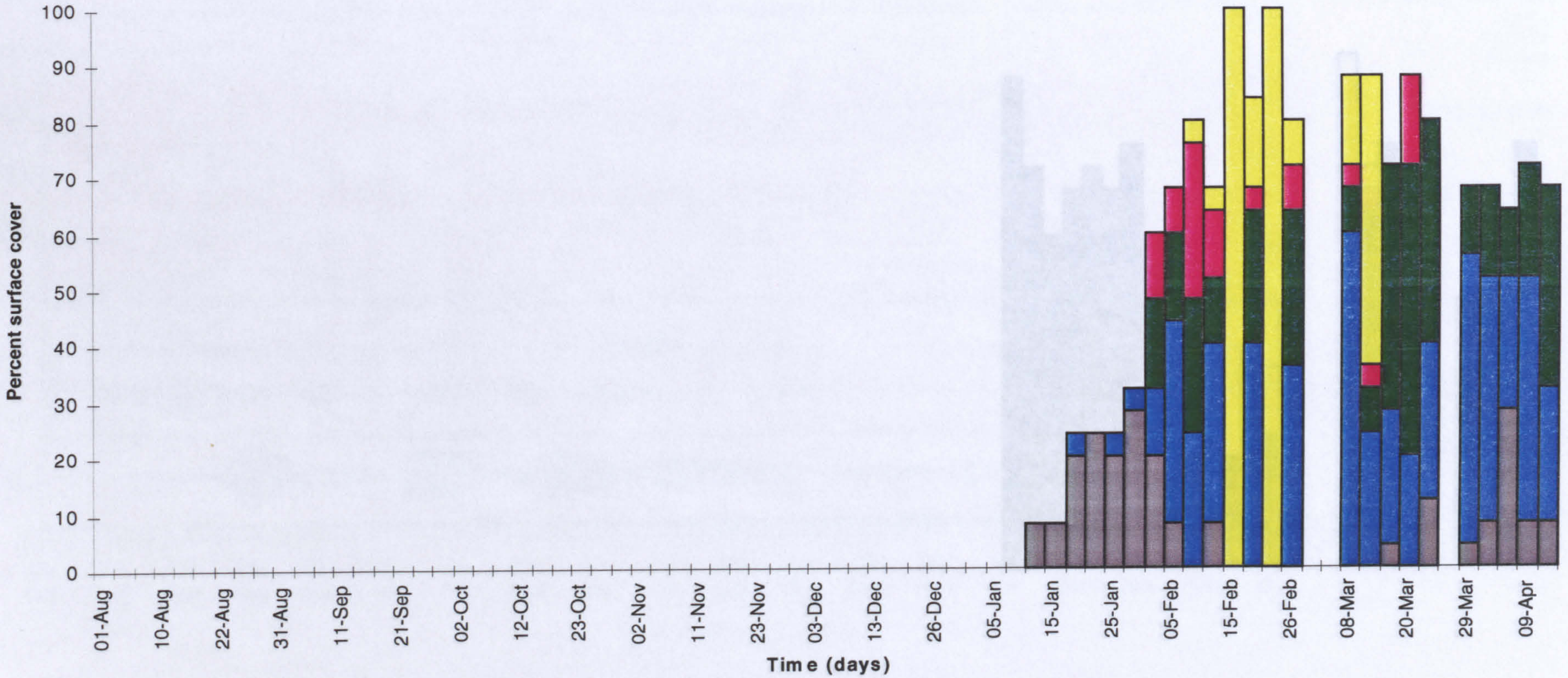


Figure 7.26: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 2 (repeat)**; SC 1 (▮), SC 2 (▮), SC 3 (▮), SC 4 (▮), SC 5 (▮).

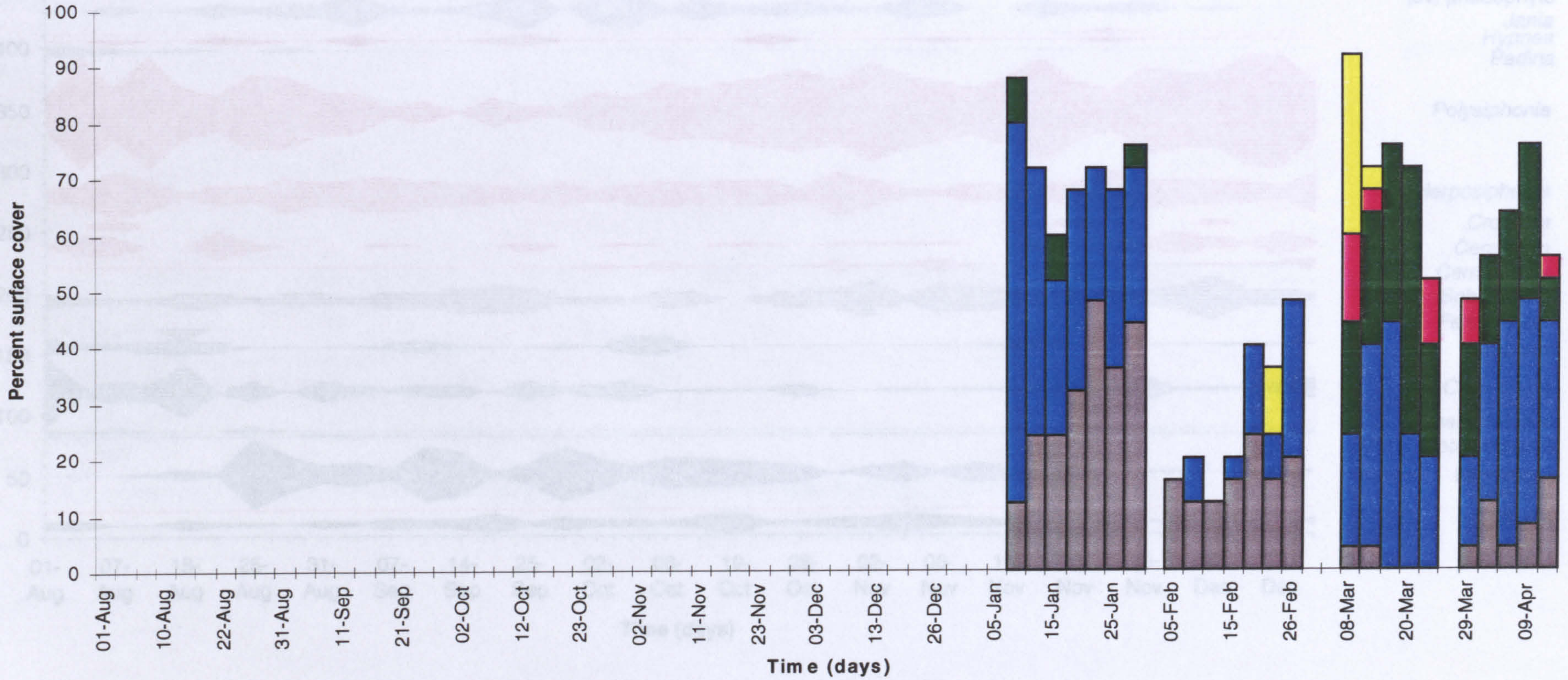


Figure 7.27: Total **percent surface cover** of different **size classes** (SC) of the algal community on **Treatment 4 (repeat)**; SC 1 (■), SC 2 (■), SC 3 (■), SC 4 (■), SC 5 (■).

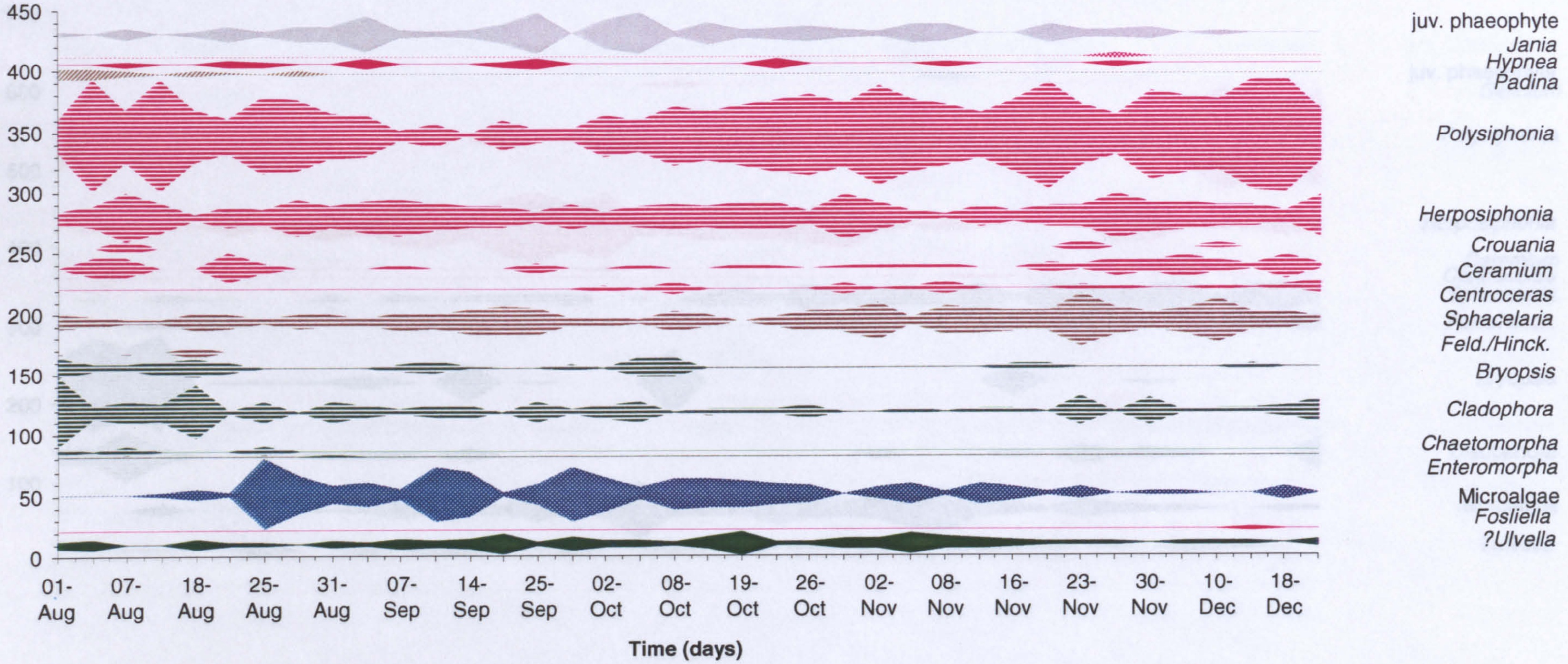


Figure 7.28: **Seasonal patterns** in the average, total volumetric cover per genus recorded on the **control treatment** replicates during **summer/autumn**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

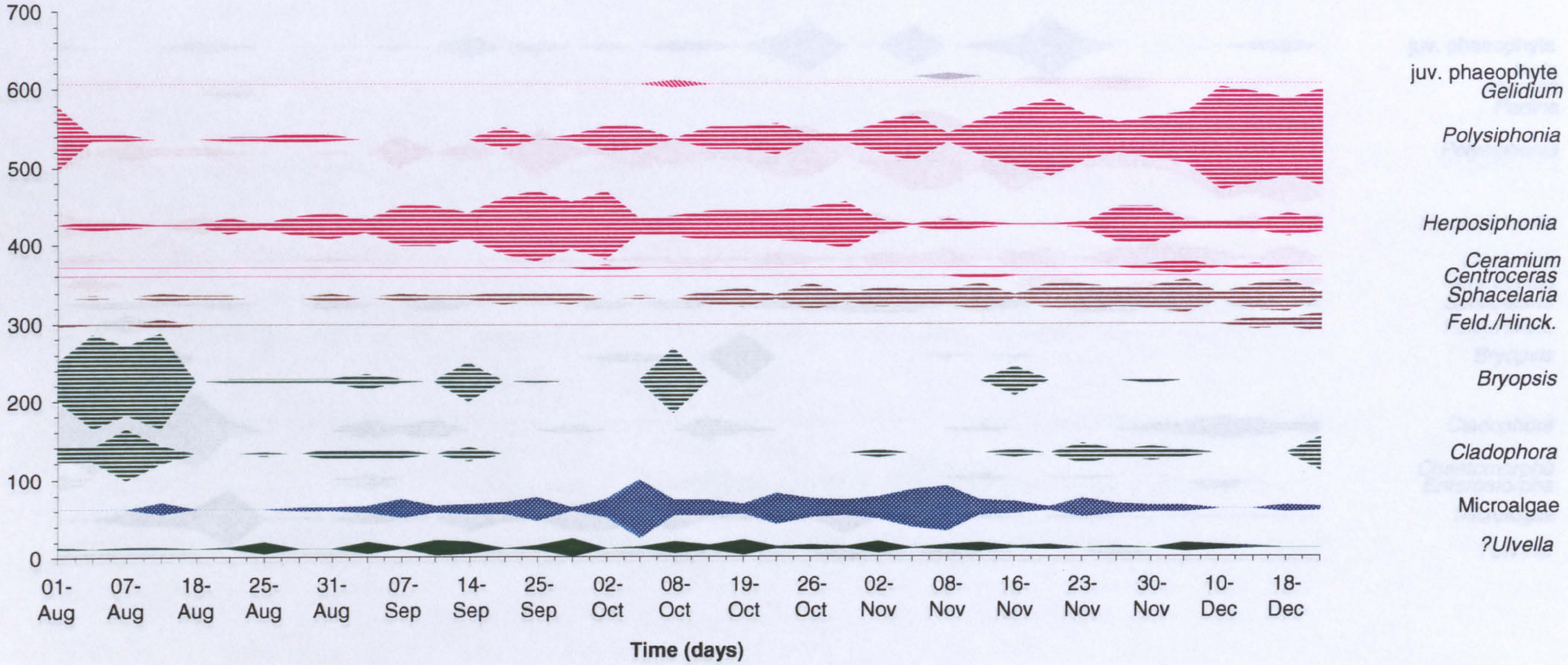


Figure 7.29: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 1**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

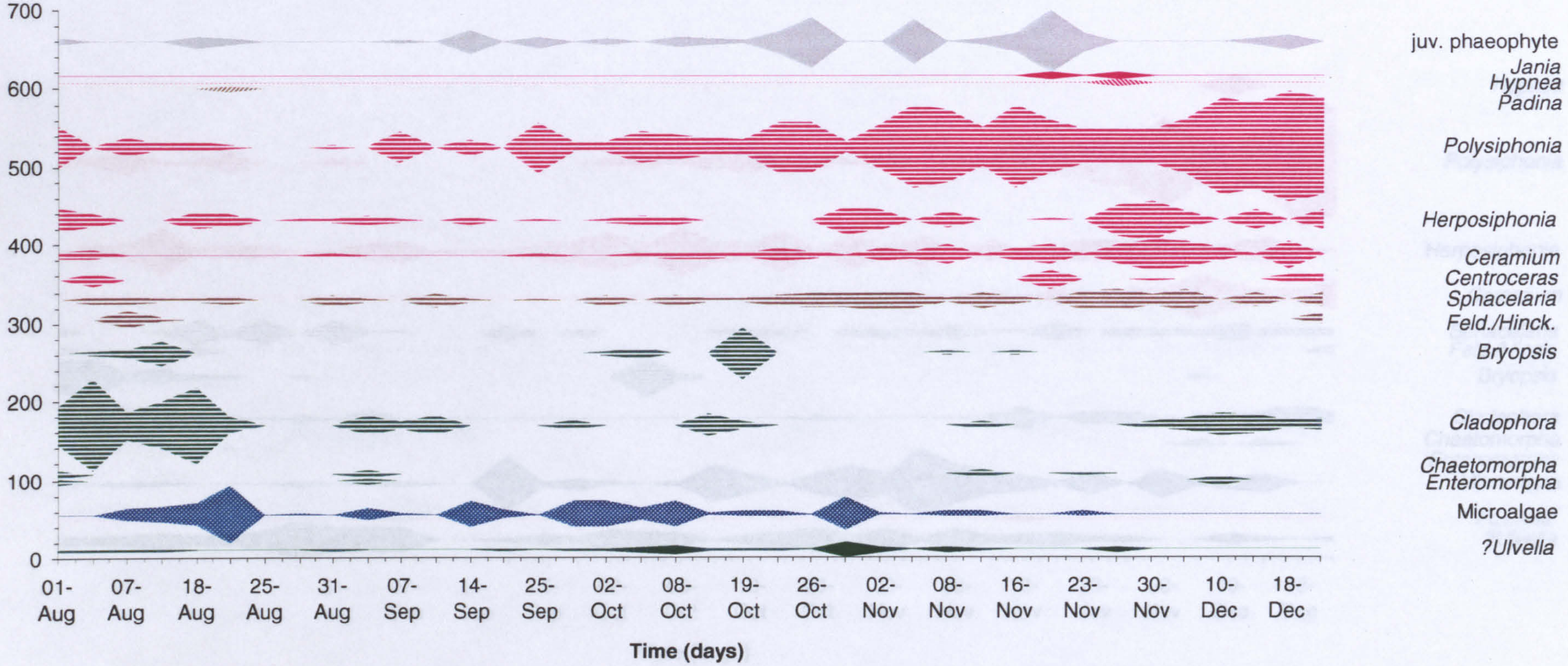


Figure 7.30: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 2**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

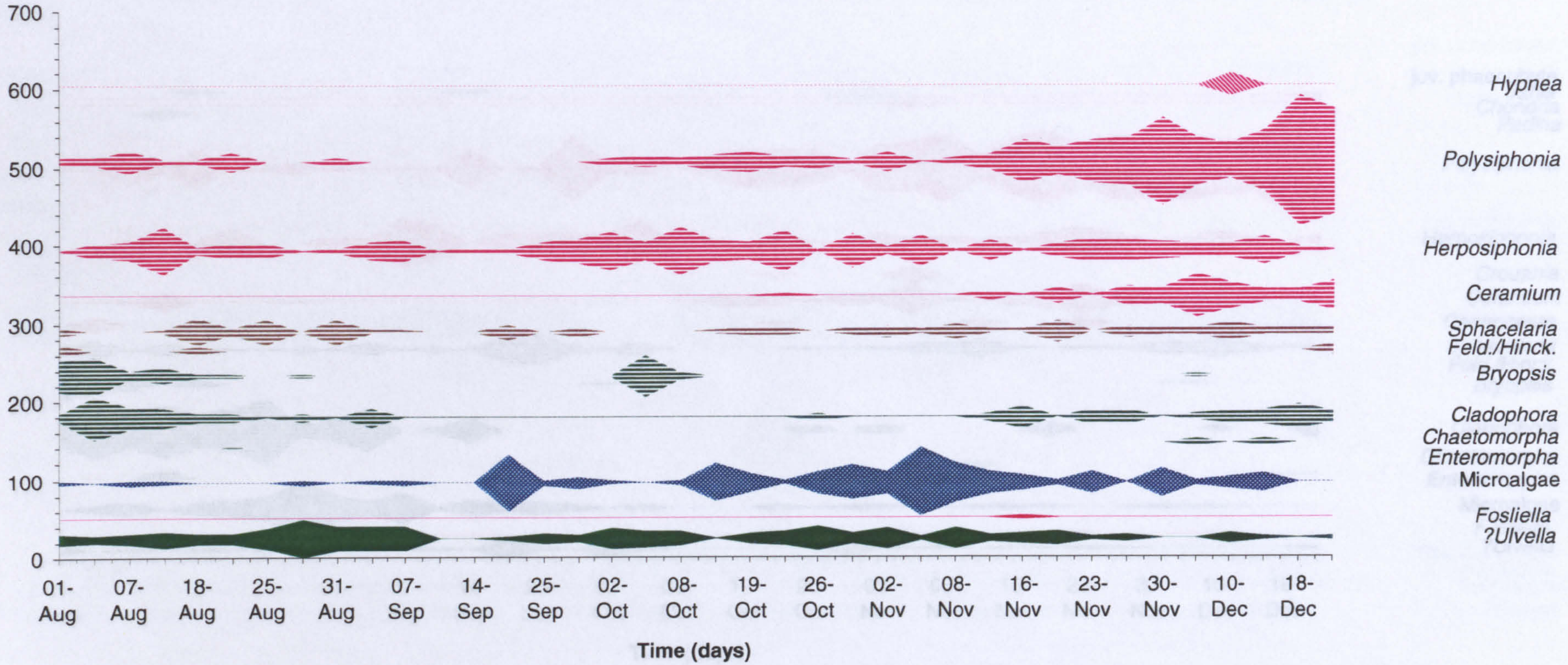


Figure 7.31: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 3**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

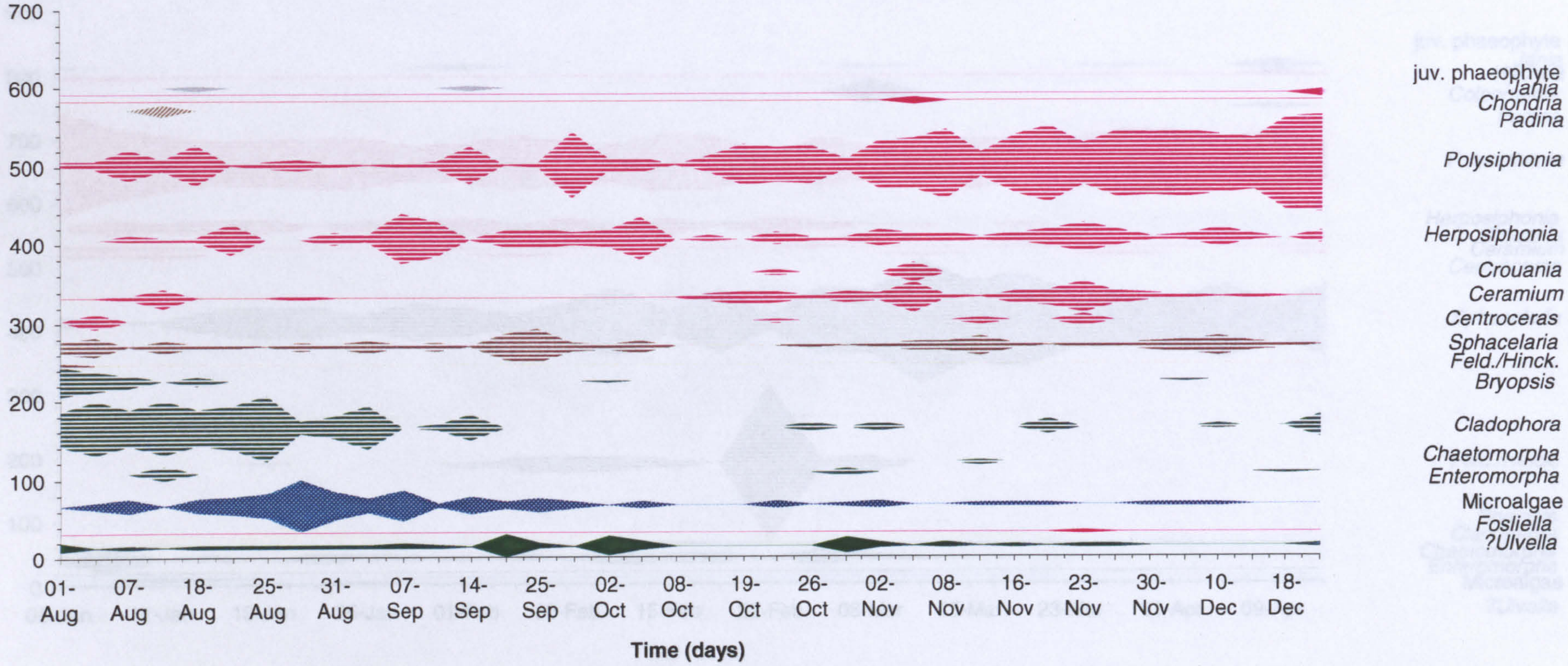


Figure 7.32: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 4**;

■crustose ▩microalgae ≡filamentous ▨corticated-foliose ▧corticated macrophytes ▦articulated calcareous ■Chlorophyta ■Phaeophyta ■Rhodophyta

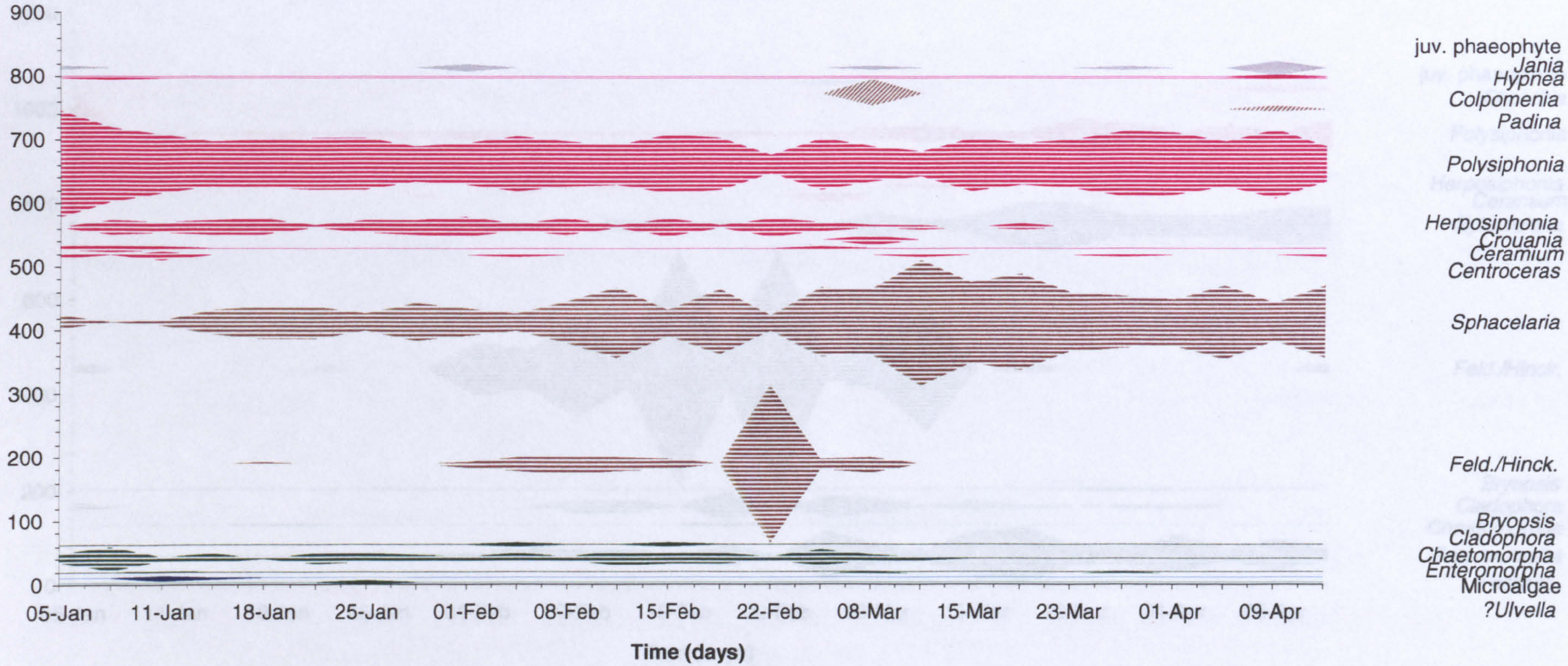


Figure 7.33: **Seasonal patterns** in the total volumetric cover per genus recorded on the **control treatment** replicates during **winter/spring**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

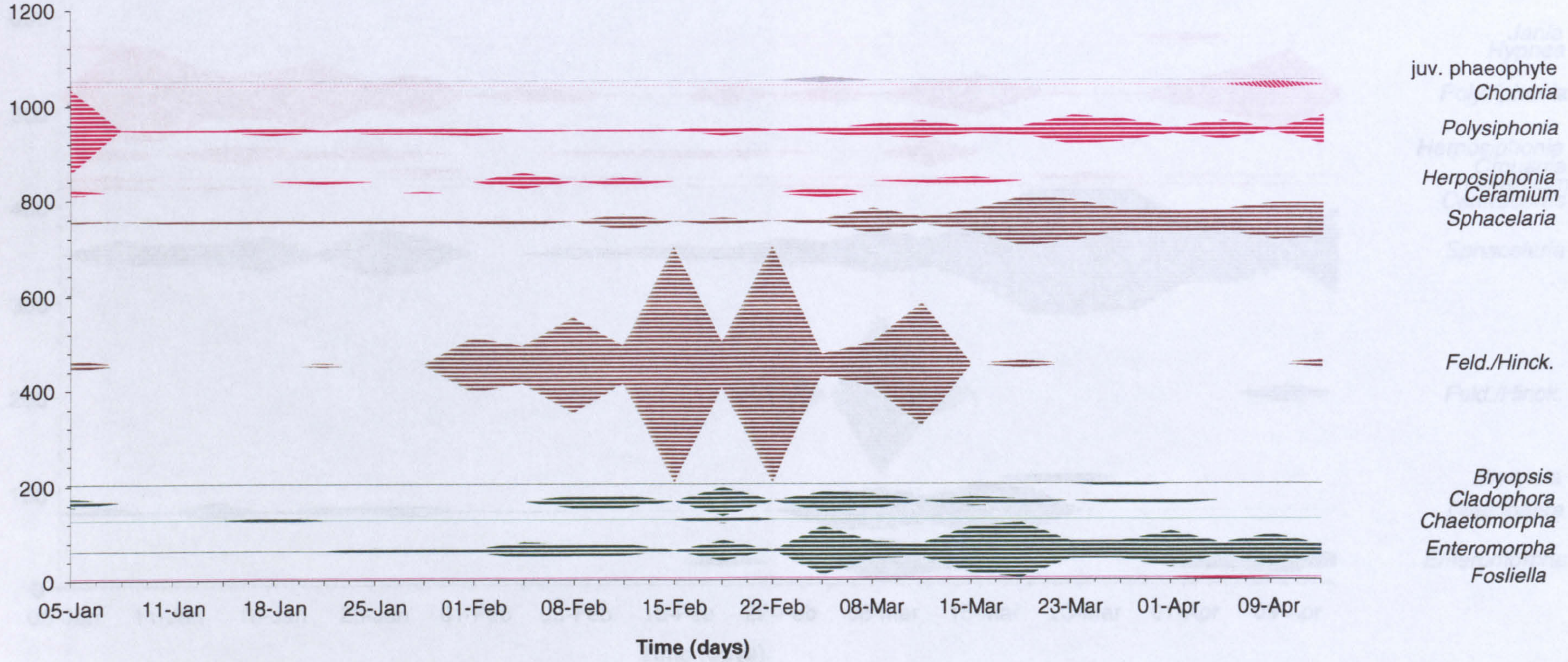


Figure 7.34: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 2 (repeat)**;

crustose microalgae filamentous corticated-foliose corticated macrophytes articulated calcareous Chlorophyta Phaeophyta Rhodophyta

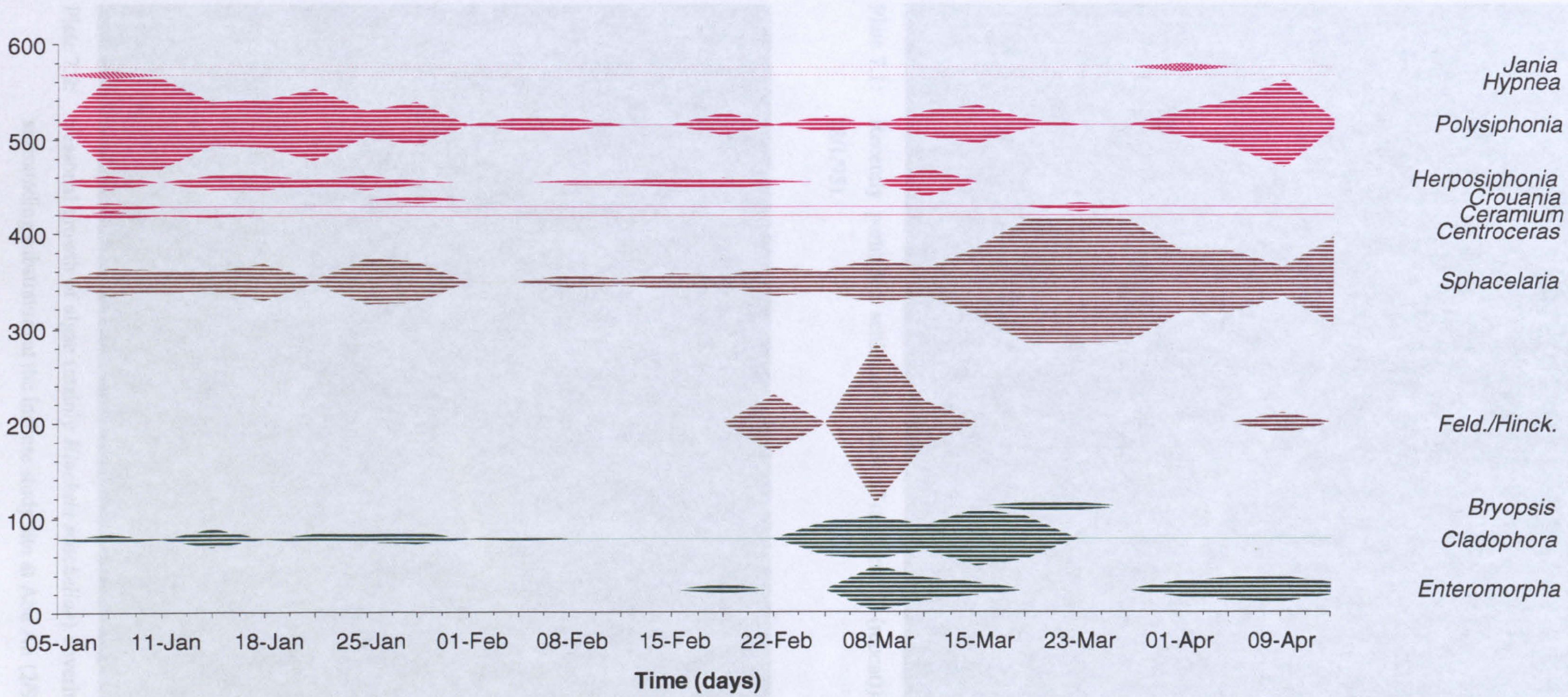


Figure 7.35: **Seasonal patterns** in the total volumetric cover per genus recorded on **Treatment 4 (repeat)**;

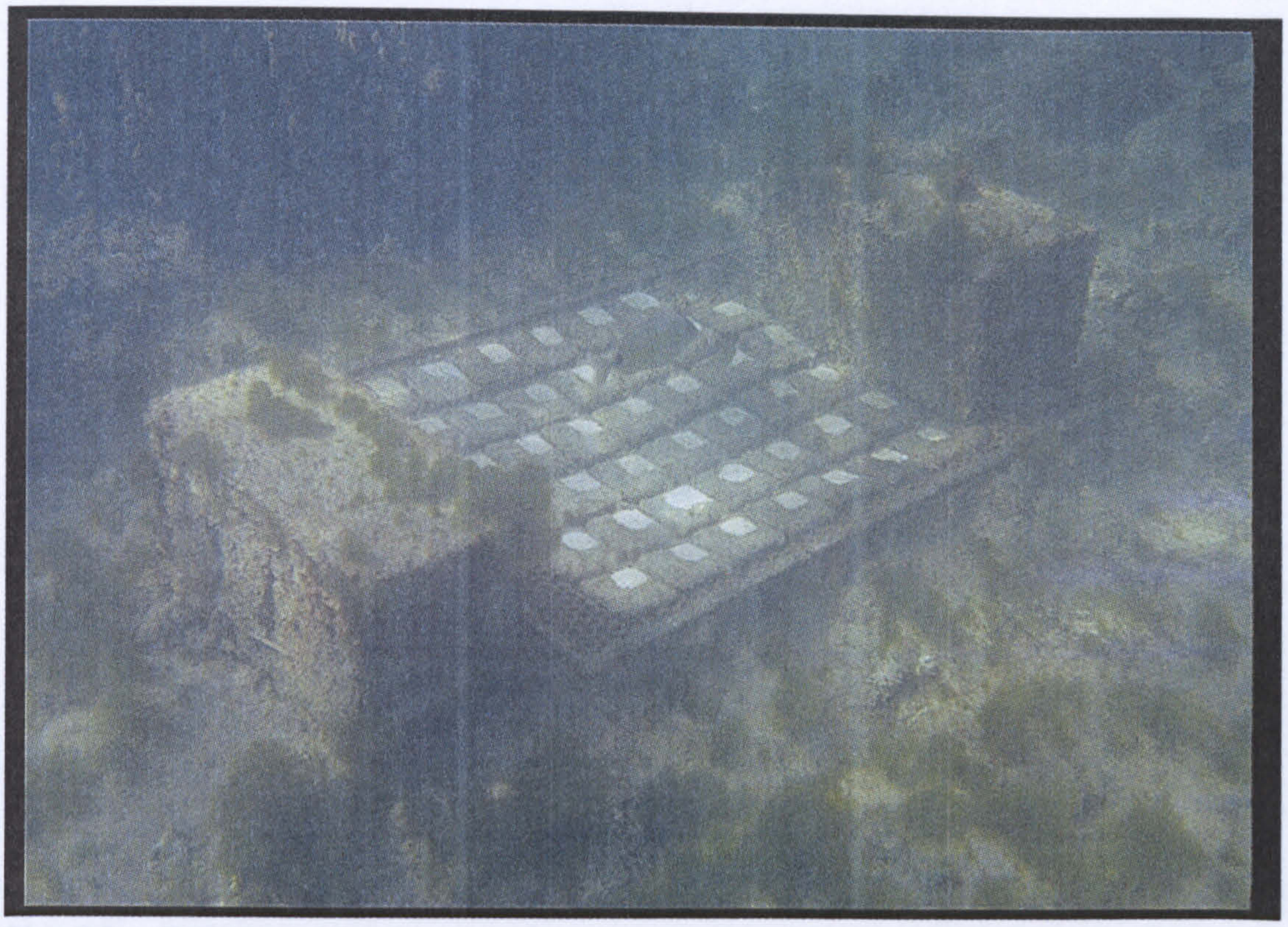


Plate 7.1: Recently perturbed settlement plates (Treatment 2 (repeat)) at the inshore study site (8/1/95).

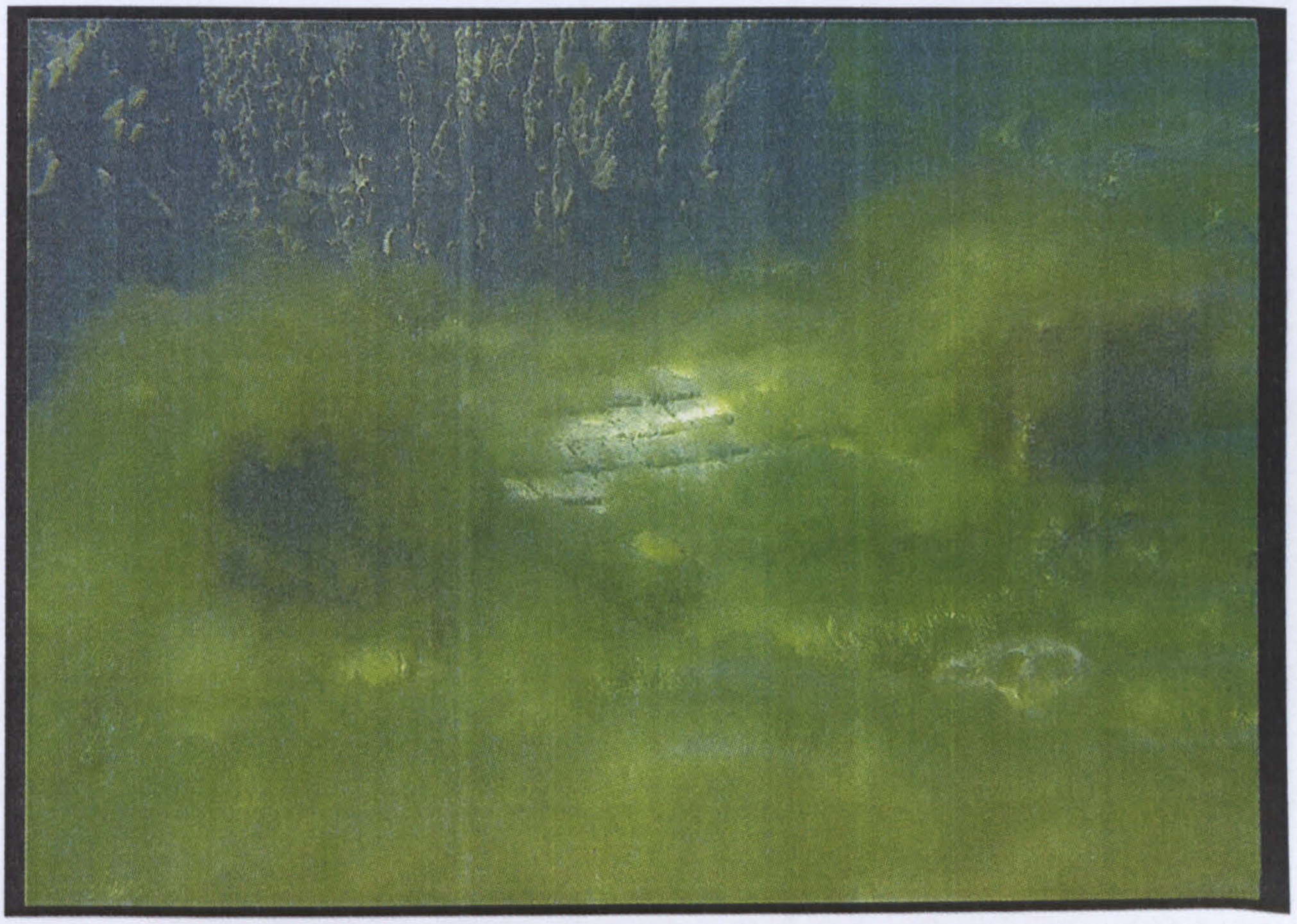


Plate 7.2: Seasonal growth of algae (mainly *Hincksia mitchellae*) covering Treatment 2 (repeat) and surrounding substratum at the inshore study site at Abu Ali (2/95).

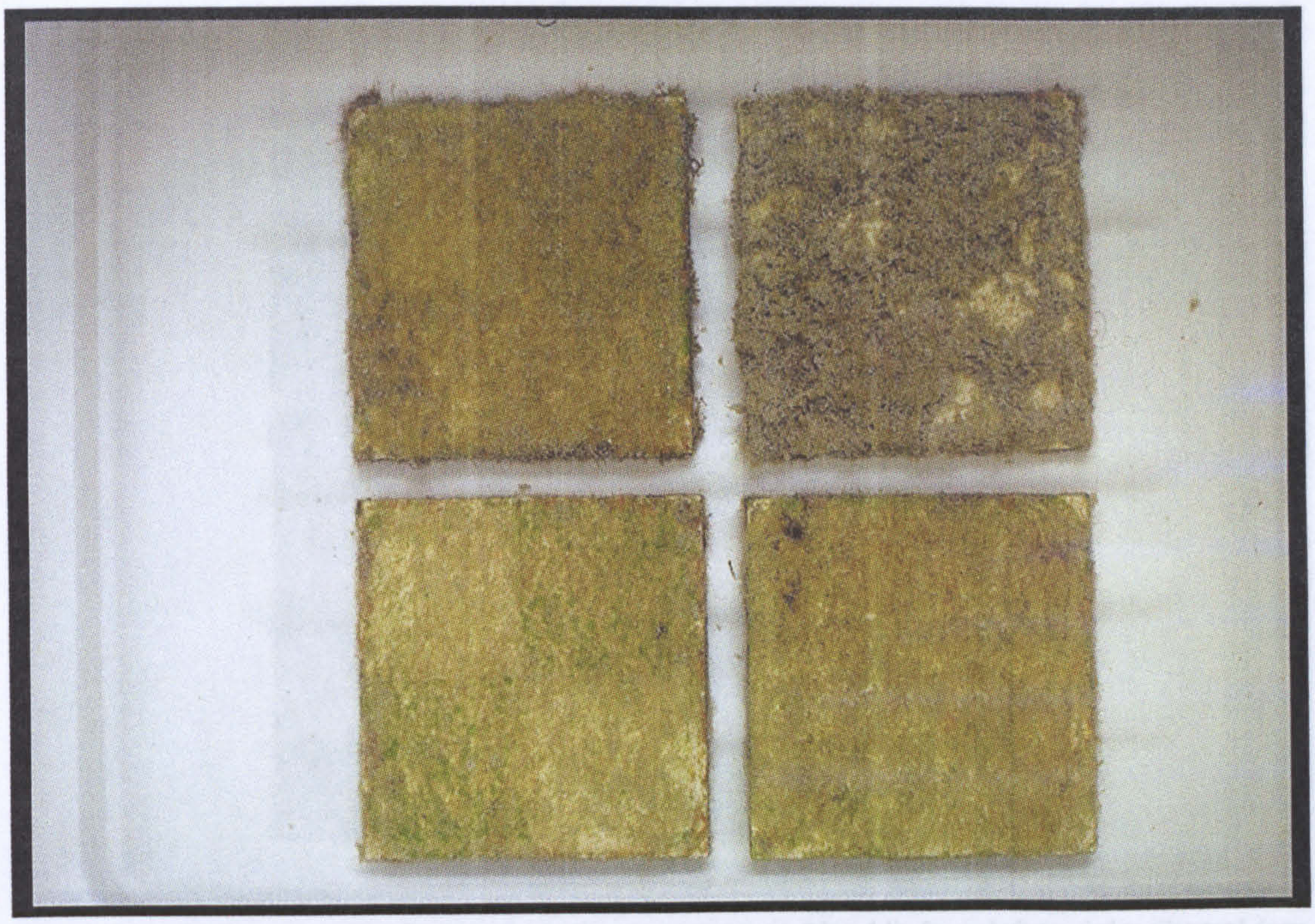


Plate 7.3: Settlement plates from perturbation treatments at Abu Ali, from left to right; T1 and T2 (top row), T3 and T4 (bottom row) (25/9/94). Perturbation impact still evident on Treatments 2 and 3. Treatment 1 has recovered and Treatment 4 has yet to be perturbed.

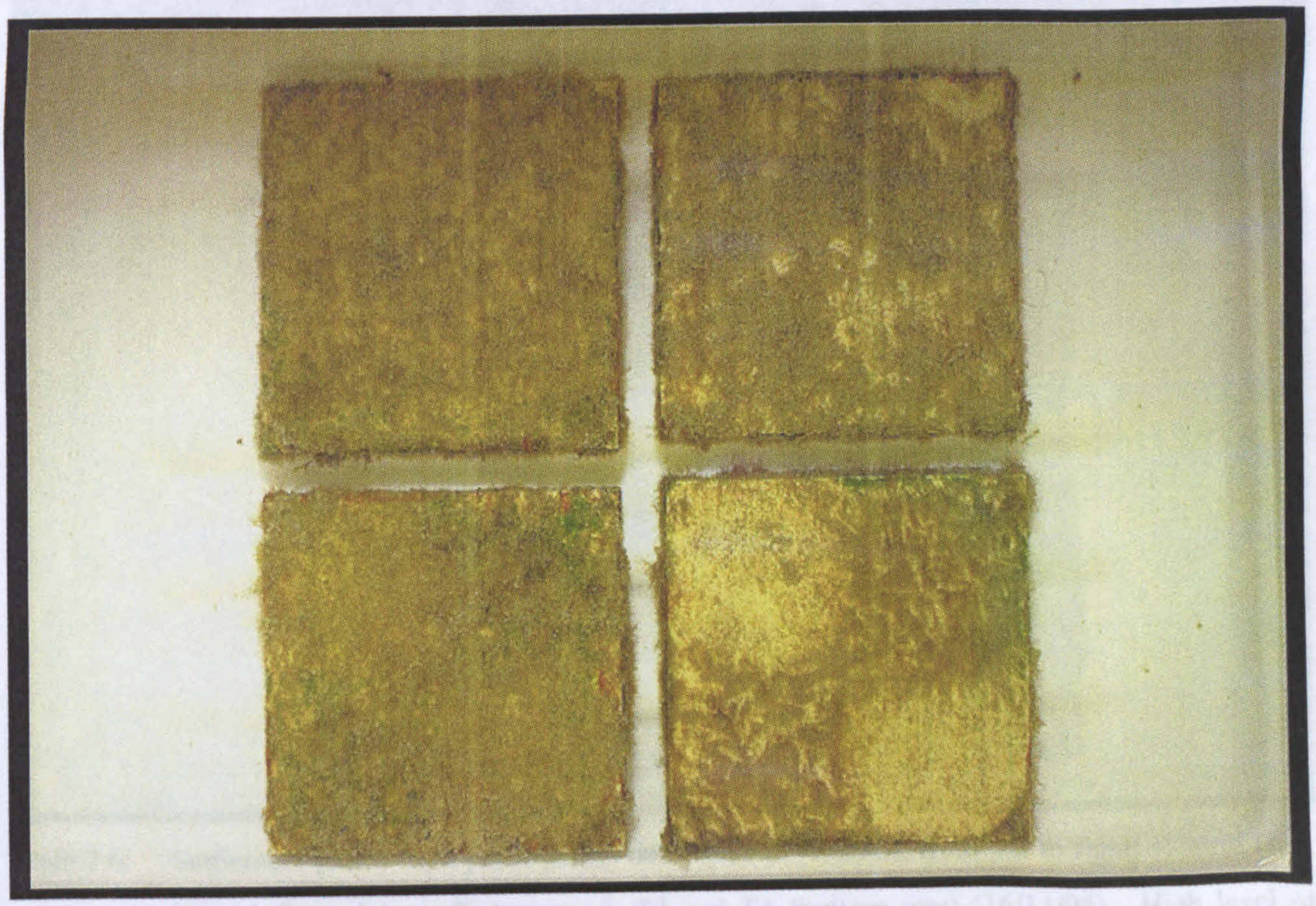


Plate 7.4: Settlement plates from perturbation treatments at Abu Ali, from left to right; T1 and T2 (top row), T3 and T4 (bottom row) (15/10/94). Treatment 4 has recently been perturbed.

Plate 7.5: Settlement plates from perturbation treatments at Abu Ali, from left to right; Control (rep. 1) and Control (rep. 2) (top row), T1 and T3 (bottom row) (15/10/94). Perturbed treatments have re-attained a similar level of algal cover shown by the control replicates.

Plate 7.6: Settlement plates from perturbation treatments at Abu Ali, from left to right; Control (rep. 1) and Control (rep. 2) (top row), T2 and T4 (bottom row) (16/11/94). High level of sedimentation covering all settlement plates.

Plate 7.7: Settlement plates (partially washed) from perturbation treatments at Abu Ali, from left to right; T1 (Ch 5) and Control (rep. 1) (top row), T2 and T4 (bottom row) (8/2/94). Treatment 4 (repeat) has recently been perturbed, and Treatment 2 (repeat) shows initial colonisation by *Feldmannia/Hincksia* spp.

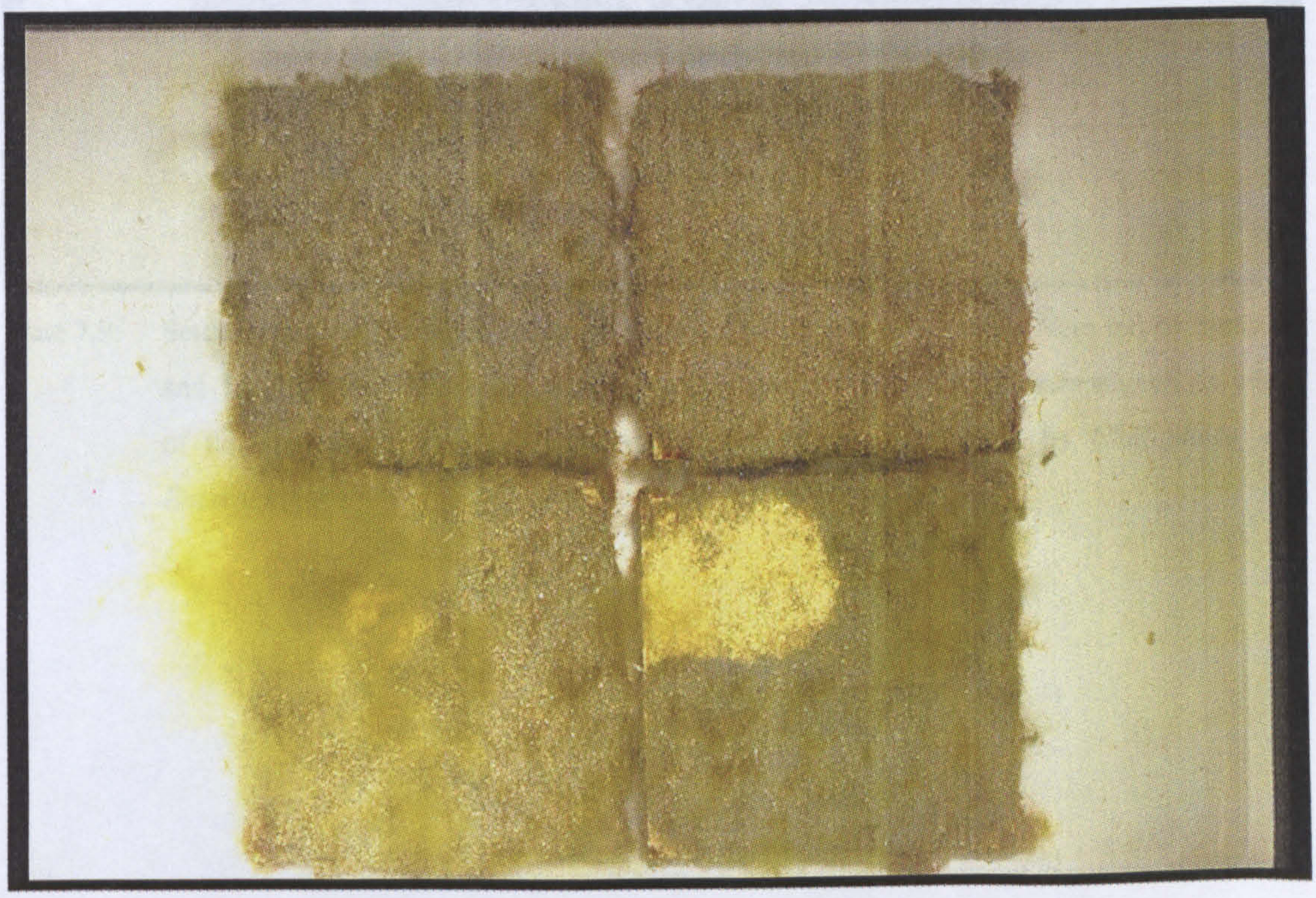


Plate 7.8: Settlement plates from perturbation treatments at Abu Ali, from left to right; Control (rep. 1) and Control (rep. 2) (top row), T2 and T4 (bottom row) (15/2/94). Treatment 2 (repeat) has developed a large standing crop of *Feldmannia/Hincksia* spp.

SECTION FOUR

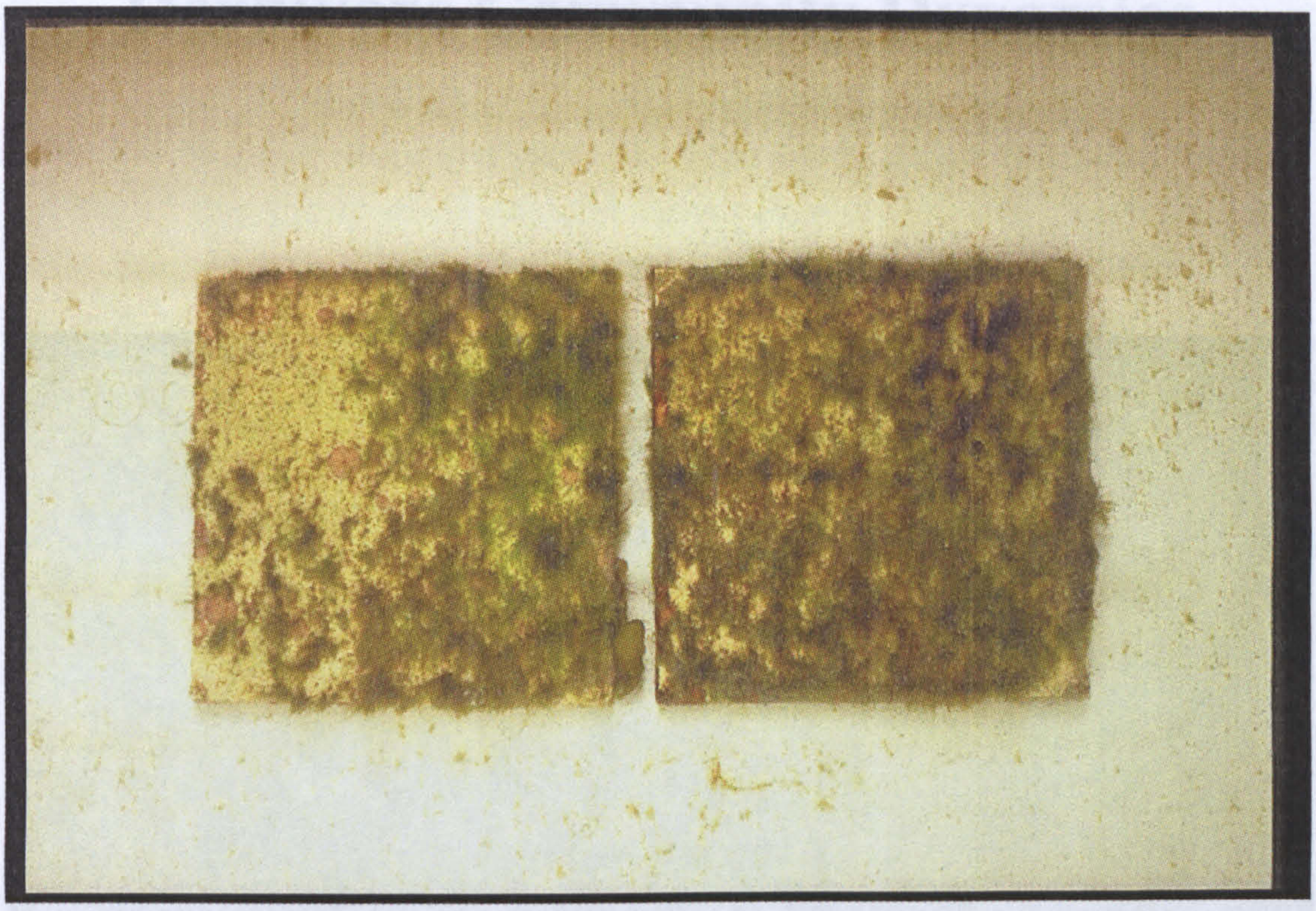


Plate 7.9: Settlement plates (washed) from perturbation treatments at Abu Ali, from left to right; T4 and T4 (13/4/94). External perturbation (i.e. abrasion by adjacent macroalgae), on edges of the settlement plate has resulted in increased re-colonisation by *Cladophora* and *Enteromorpha* spp.

SECTION FOUR

Herbivore Community Dynamics

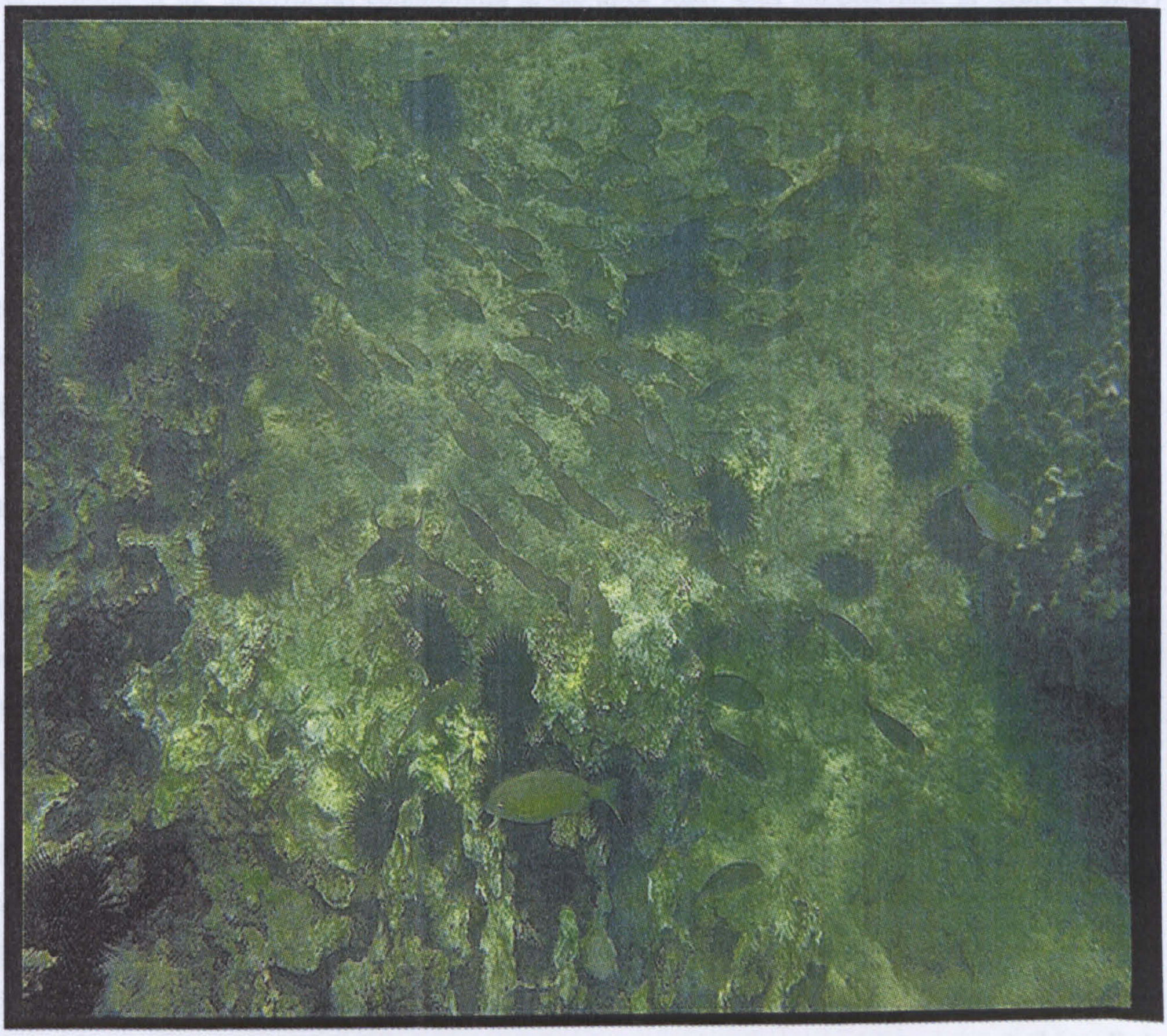


Plate 8.0: *Echinometra mathaei* and *Siganus* spp. at Abu Ali (8/94).

Chapter Eight

Fish and Echinoid Dynamics

Summary

Herbivorous fish and echinoid communities at the three study sites were monitored throughout the 12-month study period. At the inshore fringing reef, maximum fish abundance occurred during summer, with a dramatic reduction during the winter season, and was dominated by rabbitfish, *Siganus* spp. Similar trends in seasonal abundance were observed at the shallow and deep offshore sites, the former dominated by parrotfish, *Scarus* spp., and the latter by damselfish, *Pomacentrus* spp. The echinoid community at the inshore site consisted exclusively of *Echinometra mathaei*, with a mean density of 6.5 ± 0.42 m^{-2}. Due to logistical constraints, only one estimate of the echinoid community at the deep offshore study site was made, revealing *Diadema setosum* at a mean density of 0.68 m^{-2}. The composition of the herbivorous communities at the three study sites are described in terms of their grazing effectiveness.

8.1 Introduction

The herbivore community of a coral reef is as diverse as it is abundant, comprising an important part of the reef fauna. Considering reef fishes alone, it has been estimated that up to 35 % of the species diversity and biomass is attributable to herbivorous fishes (Ogden and Lobel, 1978; Sutton, 1983). It is also widely acknowledged that grazing echinoids and herbivorous fish, especially scarids and acanthurids, play important roles in the regulation of the algal community (Steneck, 1988) and the reef structure and integrity through bioerosion (Hutchings, 1986). Furthermore, the classification of the herbivore community either in terms of their foraging ranges (Carpenter, (1983) or their grazing effectiveness (Steneck, 1988) has allowed researchers to examine their differential effects on the reef community. The composition of the herbivore community can also be used to provide insights of the status of the reef health and carrying capacity, as well as the impacts of any external factors such as fishing effects (Jennings and Lock, 1996).

The systematics, biogeography and aspects of the ecology of echinoderms inhabiting the Gulf have been extensively covered by Price (1981, 1982a,b, 1983; Price and Rezai, 1996). Despite records of about 100 species for the region, only two are important herbivores of the reef community. Firstly, *Echinometra mathaei*, a small, rock-boring urchin ubiquitous to the Indo-Pacific (Khamala, 1971) and, secondly, *Diadema setosum*, a large, long-spined urchin and a close relative of the extensively studied *D. antillarum* (Sammarco, 1982a,b; McClanahan and Muthiga, 1988; Levitan 1991b). Previous studies have also recorded a range of fish assemblages inhabiting the reefs in the Gulf. Smith *et al.* (1987) recorded only 72 species off the coast of Bahrain and Downing (1985) found 85 species on Kuwaiti

reefs, while McCain *et al.* (1984) and Coles and Tarr (1990) found 106 and 101 species respectively off the east coast of Saudi Arabia. A more recent study on the Saudi Arabian reefs by Krupp and Almarri (1996) has increased the number to 281 species.

The aim of this study, using similar methodologies used by previous workers in the area, was to monitor, describe and assess throughout a 12-month period the herbivorous fish and echinoid communities inhabiting Saudi Arabian inshore and offshore coral reefs. This provides a means of estimating the relative potential impact, both spatially and temporally, of their grazing activities on the benthic algal communities.

8.2 Materials and Methods

8.2.1 Experimental design

At each study site a permanent transect, 50 m metres in length and marked by metal stakes secured to the reef at each end, was established parallel to the shore. During each count the transect was delineated by a rope, knotted at two metre intervals, that was tied between the two markers. The abundances of herbivore groups (i.e. fish and echinoids) were monitored and recorded throughout a 12-month period from May 1994 - May 1995.

8.2.2 Fish density

During each count the length of the transect was swum at a continuous pace, and the numbers of all targeted fish species occurring within a metre either side of the transect line were recorded on a pre-labelled underwater writing slate. Species targeted included all herbivorous fishes as well as selected omnivores and any known predators of echinoids. The width of the transect was visually estimated with the aid of a two metre long pole held in the middle. Censuses took place at approximately the same time of day (i.e. mid-morning). Only one count of each transect was made during each sampling period, as successive counts were deemed to be too disruptive. Whenever possible, the maximum frequency of sampling at Abu Ali and Jana Island was twice a week and twice a month respectively.

8.2.3 Echinoid density

During each count, a 1 m^2 quadrat was placed along the fifty metre transect at two metre intervals (i.e. n = 25) and the numbers of individuals contained within its confines were recorded (Plate 8.1). Whenever possible, the maximum frequency of sampling at Abu Ali and Jana Island was twice a week and twice a month respectively. At the offshore sites the dominant echinoid was *D. setosum*, and in order to obtain accurate estimates of its abundance, the counts were conducted at night, approximately two hours after sunset.

8.3 Results

8.3.1 Fish density

A total of forty-three counts were made along the fifty metre transect at the inshore study site during the 12-month period and a total of nine counts at each of the two offshore sites. There were significant differences within and between the herbivore communities at each site. Abu Ali was dominated by rabbitfish, which accounted for 92% of the herbivorous fish abundance (Figure 8.1; ANOVA (2-way without replication), $n = 172$, $p < 0.001$). *Siganus javus* and *S. canaliculatus* were the dominant species. Jana (shallow) was dominated by parrotfish, accounting for 45% of the herbivorous fish abundance (Figure 8.2; ANOVA (2-way without replication), $n = 36$, $p < 0.001$). *Scarus sordidus* and *S. ferrugineus* were predominant. Jana (deep) was dominated by damselfish, which comprised 67% of the herbivorous fish abundance (Figure 8.3; ANOVA (2-way without replication), $n = 36$, $p < 0.001$). *Pomacentrus trichourus* was the principal species.

Abundances of all herbivore groups were highest during summer and autumn months (July - November). At Abu Ali, rabbitfish were clearly the dominant herbivore group (Figure 8.4), with damselfish (*Pomacentrus aquilus*) occurring in constant numbers, and parrotfish (*Scarus persicus*) and surgeonfish (*Acanthurus sohal*) as occasional visitors (Figure 8.5) (ANOVA (2-way without replication), $n = 172$, $p < 0.001$). Of particular significance, however, is the almost complete absence of all fishes during the winter months after a sharp decline in December. Even by the early spring months (March - April) only rabbitfish were present in any significant numbers.

At both offshore sites at Jana Island, similar seasonal trends were observed, but these were less pronounced than at the inshore reef (Figures 8.6 and 8.7; ANOVA (2-way without replication), $n = 36$, $p > 0.5$ and $p > 0.1$ respectively). While at the deeper site the herbivorous fish community was clearly dominated by damselfish, abundances of the different groups at the shallow site were much more evenly distributed, equating to a higher species diversity.

8.3.2 Echinoid density

Throughout the study period a total of forty transect counts were made at the inshore study site. Changes in the average density ($n = 25$) of the *E. mathaei* population are shown in Figure 8.8. The overall population density averaged 6.50 ± 0.42 (1.32) m^{-2} (x ± 95 % confidence limits, SD in parentheses), which varied significantly over time with an observed maximum and minimum of 8.48 m^{-2} and 3.76 m^{-2} respectively (ANOVA (2-way with replication), $n = 1000$, $p < 0.001$). The abundance of the urchin population along the transect (i.e. per quadrat; Figure 8.9) also varied significantly (ANOVA (2-way with replication), $n = 1000$, $p < 0.001$).

At the shallow offshore site at Jana island, neither *E. mathaei* nor *D. setosum* were observed. Consequently, no density counts could be made. At the deep offshore site at Jana Island, the density of *D. setosum* was estimated as 0.68 m^{-2}. However this value is based on only one nocturnal transect census (21/10/94) as logistical constraints prevented further observations.

8.4 Discussion

8.4.1 Fish dynamics

The results suggest that the three study sites were dominated by different groups of herbivorous fish; the inshore study site by rabbitfish (*Siganus* spp.), the shallow offshore site by parrotfish (*Scarus* spp.) and the deep offshore site by damselfish (*Pomacentrus* spp.). Of the three, the shallow offshore site possessed greatest species richness and eveness in species abundances. It is important to note, however, that these relative dominances were based on the abundance of individuals and do not consider biomass or individual length estimates.

The results compare favourably with those from some previous studies in the same areas, but with other studies some differences are apparent (Coles and Tarr, 1990; Roberts, 1993a; Krupp *et al.*, 1994; see Table 8.1). For example, from March 1985 - March 1987, Coles and Tarr (1990) conducted a wide-ranging survey of reef fish communities along the Saudi Gulf coast, including Jana and Abu Ali Island. The inshore reef at Abu Ali was characterised by the dominance of *Siganus* spp., their estimate being identical (i.e. 92%) to that made during the present study (Table 8.1). However, while their estimate of species abundances from a deep reef site at Jana are comparable to those made in the present study, abundance estimates from the shallow site are less so due to a reported dominance by damselfish: 17% (this study) vs. 47% (Coles and Tarr, 1990). Roberts (1993a) also recorded dominance by damselfish at Jana in November 1992. This dominance seems to be characteristic of the deeper offshore study site situated at the base of the reef slope, where damselfish were recorded as being dominant in terms of species abundance: 67% (this study) vs. 52 % (Coles and Tarr, 1990). Furthermore it is evident that the 'shallow' transects of both Coles and Tarr (1990) and Roberts (1993a) were located in slightly deeper water along the reef slope, rather than the reef crest area used in the present study. Krupp *et al.* (1994) also report dominance by damselfish at Jana, although less pronounced than in the other studies, and the abundances of the other herbivorous fish groups are more comparable to those in the present study. Differences with the results from the present study, including the slight discrepancy in damselfish dominance, can be at least partially accounted for, as transects of Krupp *et al.* (1994) were established perpendicular to the shoreline and so encompassed both reef crest and reef slope habitats.

The time scales of the various studies also differed considerably. The study by Roberts (1993a) was restricted to one month (November 1992), while the results of Krupp *et al.* (1994) are an average of two

separate summer investigations (June 1992 and June 1993). Coles and Tarr (1990) conducted a two-year study, the results being an average of six sampling periods from different seasons. The present study lasted only one year, but was also conducted during different seasons with the results averaged from forty-three sampling periods from the inshore and nine sampling periods from the offshore sites. Hence comparisons can be problematic, unless sampling regimes are similar, particularly in regions such as the Gulf where there is pronounced seasonality. In addition, the transect size used by Roberts (1993a) was 50 m x 4 m, while the size in the present study and others was 50 m x 2 m.

All studies in the Gulf area concur that diversity and abundance of the reef fish community is positively correlated with depth of the reef and distance from the mainland coast. A further point is that reef fish abundance is positively correlated with reef complexity rather than live coral cover (Roberts and Ormond, 1987; Coles and Tarr, 1990). In addition, the seasonally environmental extremes of the region are primarily responsible for the observed level of diversity, particularly temperature and salinity (Coles and Tarr, 1990).

Seasonal changes in abundance recorded during the present study were also observed by both McCain *et al.* (1984) and Coles and Tarr (1990). They recorded maximum abundances during summer and autumn, with a decline during winter, particularly on the inshore reefs. The seasonal increase in abundance has been attributed to the colonisation of reef areas by juveniles and sub-adults and their subsequent increase in length (McCain *et al.*, 1984). For the offshore reefs, Coles and Tarr (1990) and Roberts (1993a) suspect such increases to be linked to recruitment, but found no direct evidence. However the replenishment of the inshore reefs after the winter depopulation was almost totally by juveniles (McCain *et al.*, 1984; Roberts, 1993a; pers. obs.). Coles and Tarr (1990) suggest the annual loss of reef fish on the inshore reefs is due to their migration to other areas in response to the extreme environmental conditions, namely the lowering water temperature. The idea of migration from the shallow inshore reefs was supported by an observed increase in abundance on the shallow offshore reefs. However, Krupp *et al.* (1994) dismiss this suggestion due to the large distances involved and the fact that the majority of the Gulf benthos is sand-dominated, with few refuge areas and therefore prospective migrants would face too high a risk of predation. Instead mortality due to the decreased water temperature is proposed as being responsible for the annual depopulation of the inshore reefs. This annual 'extinction' is supported by the observed re-colonisation by juveniles. Indeed such mortality was observed during this study; the strand-line of the beach at Abu Ali was littered with dead reef fish immediately after the sharp decline in water temperature during December. However this die-off mainly consisted of primary reef fish, such as *Pomacentrus*, *Chaetodon* and *Apogon*, while transient fish such as *Rhabdosargus* and *Diplodus* were noticeably absent.

It is therefore proposed that while a significant annual mortality of primary reef fish does occur, transients, especially those with schooling behaviour, must migrate to other areas. Exactly where is not clear, and as the offshore reefs are a considerable distance away, coastal migration to possibly deeper

inshore reefs is suggested. Furthermore, the considerable industrial development of the Gulf area has led to an extensive network of submerged oil platforms and pipelines. These may provide refuges and food resources (from the colonisation of benthic flora and fauna), and even act as 'corridors' facilitating migrations across the relatively barren, sand-dominated benthos. Indeed, the attraction of reef fish to submerged artificial structures is well documented (Basson *et al.*, 1977; Downing *et al.*, 1985; Polovina, 1991).

The inshore reef areas may also function as nursery grounds and potential sources of recruits. For example, the extensive population of *Siganus* spp. at Abu Ali, after an initial increase, exhibited a steady decline in abundance that corresponded with an increase in size as the juveniles subsequently matured during the study period (pers. obs.). Predation would have been partially responsible for this observed decline but it may also be correlated with changing environmental conditions. For example, the seasonal growth and decline of benthic macro-algae, such as *Colpomenia* and *Sargassum* spp (see Chapter 5). McCain *et al.* (1984) observed a correlation between fish abundance and macroalgal cover on the inshore reefs, particularly for the transient, *Rhabdosargus haffara*. In the present study a similar correlation was observed with the transient *Diplodus sargus*, with a dramatic decline after the loss of macroalgal cover during the early summer months. Indeed it may be that the macroalgal blooms provide habitats for new recruits, supplying refuges and food resources. The new recruits subsequently migrate to other areas, such as seagrass beds, upon the macroalgal decline. This hypothesis is supported by the observation of large aggregations of *Diplodus sargus* fry amongst the extensive stands of *Sargassum boveanum* at Abu Ali during the spring months (March - April 1995). It is important to note that the above observations have only considered transient species and their dynamics from the spring season onwards. The use of macroalgae then seagrass as a nursery habitat for other species, such as the commercial shrimp *Penaeus semisulcatus*, has also been reported in the Gulf (Basson *et al.*, 1977). Overall the abundance of the herbivorous reef fish community during the present study, at the inshore reefs in particular, was negatively correlated with macroalgal abundance during the winter season (but with a subsequent increase during the spring). This may be due to mortality or reduced foraging activity in response to the lower temperatures (Hatcher, 1981; McCain *et al.*, 1984). The loss in herbivore abundance may subsequently initiate a macroalgal bloom or the latter may be entirely an abiotic related phenomenon. Unfortunately, for the Saudi Gulf coast reefs, no direct data exist to clarify whether the seasonal changes in the abundance of reef fish groups and individual species is linked to macroalgal blooms, abiotic conditions or both.

8.4.2 Echinoid dynamics

The mean abundance of *E. mathaei* on the fringing reef along Abu Ali Island over the entire study period was 6.5 m^{-2}. Despite appreciable variance, temporal changes were significant, with a maximum during summer and a minimum during winter (Figure 8.8). Mortality in winter due to predation, recruitment and/or environmental conditions could all have been partially responsible for the observed

population dynamics. Few fish predators were recorded during the censuses, so this factor is unlikely to be of importance. Similarly, recruitment would also seem an unlikely factor due to the absence of juveniles observed during the summer months. Therefore, the influence of environmental factors, particularly temperature and especially the adverse effects of cold winter temperatures, was probably important. During this period, individuals were observed half-buried in the sand area behind the fringing reef, either dead or unresponsive. These had possibly been swept from the reef once they had died or reached a weakened state.

Possible sources of sampling bias include obscurement of *E. mathaei* by macroalgae, which was more prevalent in the winter/spring than the summer. Counts might therefore have been underestimates in winter/spring, and the summer density peak partly an artefact.

Hence the overall average population density of 6.5 individuals per m^2 may well be an underestimate and the true value could be nearer to 8 individuals per m^2. Other studies of echinoid populations along Abu Ali, particularly by Vogt (1994a,b; 1996) have recorded a similar average density, but this author also encountered similar biases in sampling technique due to the influence of seasonal growth by algae. Richmond (1994; 1996) recorded *E. mathaei* populations on a nearby patch reef in the order of 30 individuals m^{-2} (although this was based on only one sampling period), an estimate comparable to the high density populations of *E. mathaei* recorded by Downing and El-Zhar (1987) on the fringing reefs surrounding islands of Kuwait.

The shortage of quantitative data from the offshore studies prevented any direct comparison with the inshore site. Furthermore, the apparent absence of *E. mathaei* from the shallow offshore site suggested a very patchy distribution, possibly due to a high predation pressure in this zone of the reef, and results of the fish censuses did indicate the presence of predators. Limited survey of the windward side of the island revealed the presence of *E. mathaei*, but these were very small individuals compared to those of the inshore reef and all were confined to enclosed burrows. These are signs of high predation pressure (McClanahan and Kurtis, 1991) and/or a high abundance of drift food (Hart and Chia, 1990). Furthermore, only one individual of *D. setosum* was observed at the shallow site, although this was during the day and a nocturnal count would conceivably have produced higher numbers. *D. setosum* seemed more abundant at the deeper site, perhaps due to reduced wave exposure and/or predation pressure. However its density was much lower than anticipated (0.68 individuals m^{-2}), but this estimate was based on only one nocturnal count.

8.4.3 Differential grazing pressure

The range of different herbivorous organisms found on a coral reef, from microherbivores to echinoids and fish, can be classified in terms of their effectiveness at grazing the algae growing on the reef substrate (Steneck, 1988; Chapter 2). Applying this functional approach to the data collected during the

present study provides at least a qualitative estimate of the different grazing regimes operating at the three study sites. For example, the herbivorous fish community on the inshore fringing reef at Abu Ali was dominated by *Siganus* spp. which have been classed as *denuding* herbivores; they can significantly reduce algal biomass when in sufficient numbers, but are unable to remove crustose coralline algae and thereby greatly impact the reef substratum. In contrast, the shallow offshore site at Jana island was characterised by *Scarus* spp. which are defined as *scraping* herbivores; they have the greatest impact on algal abundance being able to feed on the widest range of algal types, including crustose corallines and can thereby impact the reef substrate as well. The deep site at Jana however, was dominated by *Pomacentrus* spp. which are classed as *non-denuding* herbivores; they have a limited ability to reduce algal biomass. The *E. mathaei* at the inshore site are also classed as *scraping* herbivores.

Hence it can be seen that the relative dominance of the different herbivorous groups would have had a differential effect on the algal community at the three study sites (i.e. the shallow offshore reef supported the most effective grazing community). Its implications are discussed further in Chapter 11.

Abu Ali	Coles and Tarr (1990)		(This study)	
	Nos.	%	Nos.	%
Damselfish	2.0	7.94	2.56	6.26
Parrotfish	0	0	0.47	1.15
Surgeonfish	0	0	0.21	0.51
Rabbitfish	23.2	92.06	37.63	92.08

Jana (shallow)	Coles and Tarr (1990)		Roberts (1993)		Krupp *et al.* (1994)		(This study)	
	Nos.	%	Nos.	%	Nos.	%	Nos.	%
Damselfish	31.4	46.59	40.7	47.83	16.22	24.00	7.67	16.92
Parrotfish	17.1	25.37	18.7	21.97	23.2	34.33	20.33	44.84
Surgeonfish	10.2	15.13	10.0	11.75	15.82	23.41	10.78	23.77
Rabbitfish	8.7	12.91	15.7	18.45	12.34	18.26	6.56	14.47

Jana (deep)	Coles and Tarr (1990)		(This study)	
	Nos.	%	Nos.	%
Damselfish	30.7	52.21	21.78	66.89
Parrotfish	16.7	28.40	6	18.43
Surgeonfish	7.2	12.25	4.67	14.34
Rabbitfish	4.2	7.14	0.11	0.34

Table 8.1: **Comparison of the herbivorous fish community** recorded at the three island sites with the results from similar studies in the same areas.

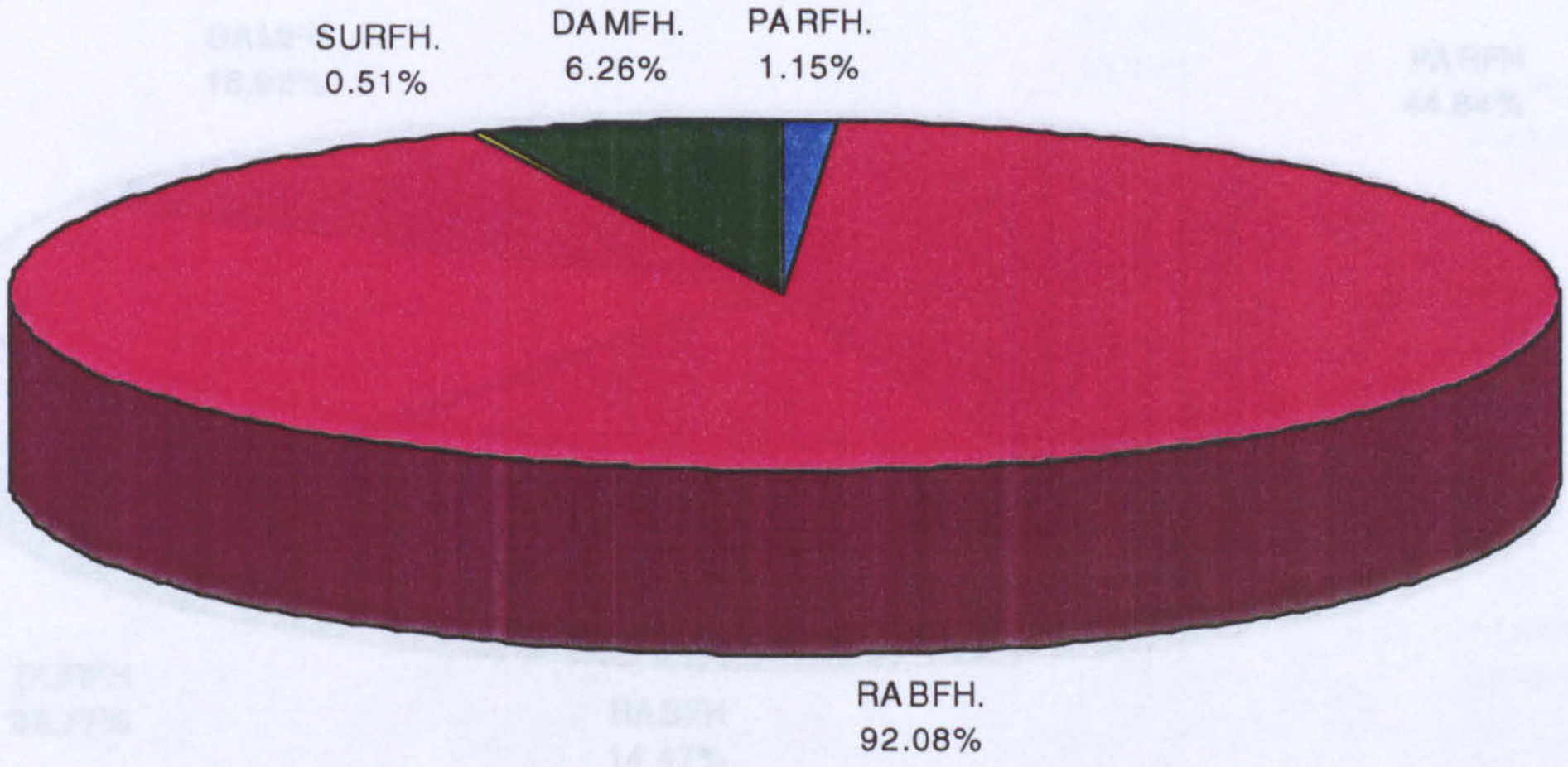


Figure 8.1: Composition of the **herbivorous fish** community at **Abu Ali** based on average abundance recorded along the 50 m transect throughout the study period; PARFH = parrotfish, RABFH = rabbitfish, SURFH = surgeonfish, DAMFH = damselfish.

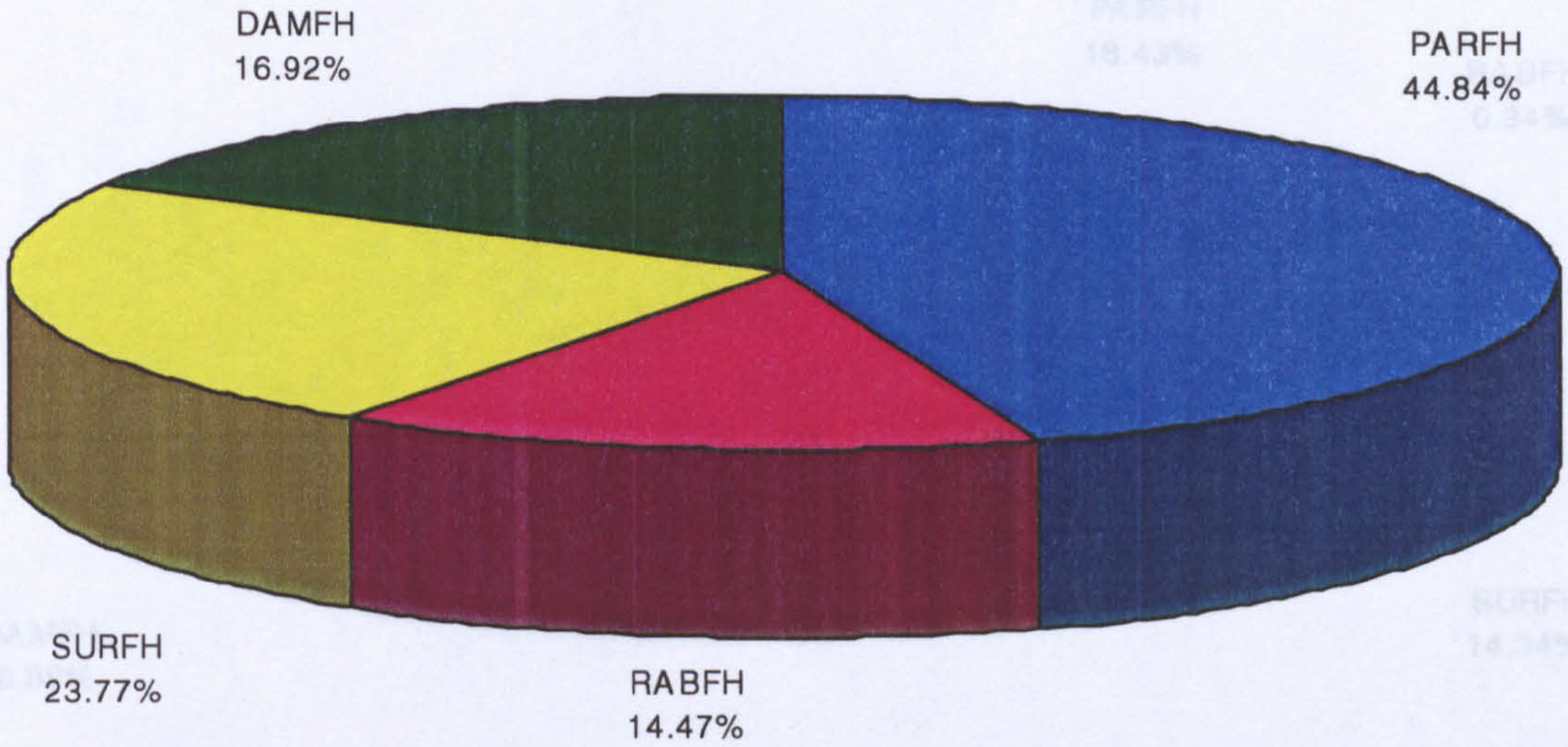


Figure 8.2: Composition of the **herbivorous fish** community at **Jana (shallow)** based on average abundance recorded along the 50 m transect throughout the study period; PARFH = parrotfish, RABFH = rabbitfish, SURFH = surgeonfish, DAMFH = damselfish.

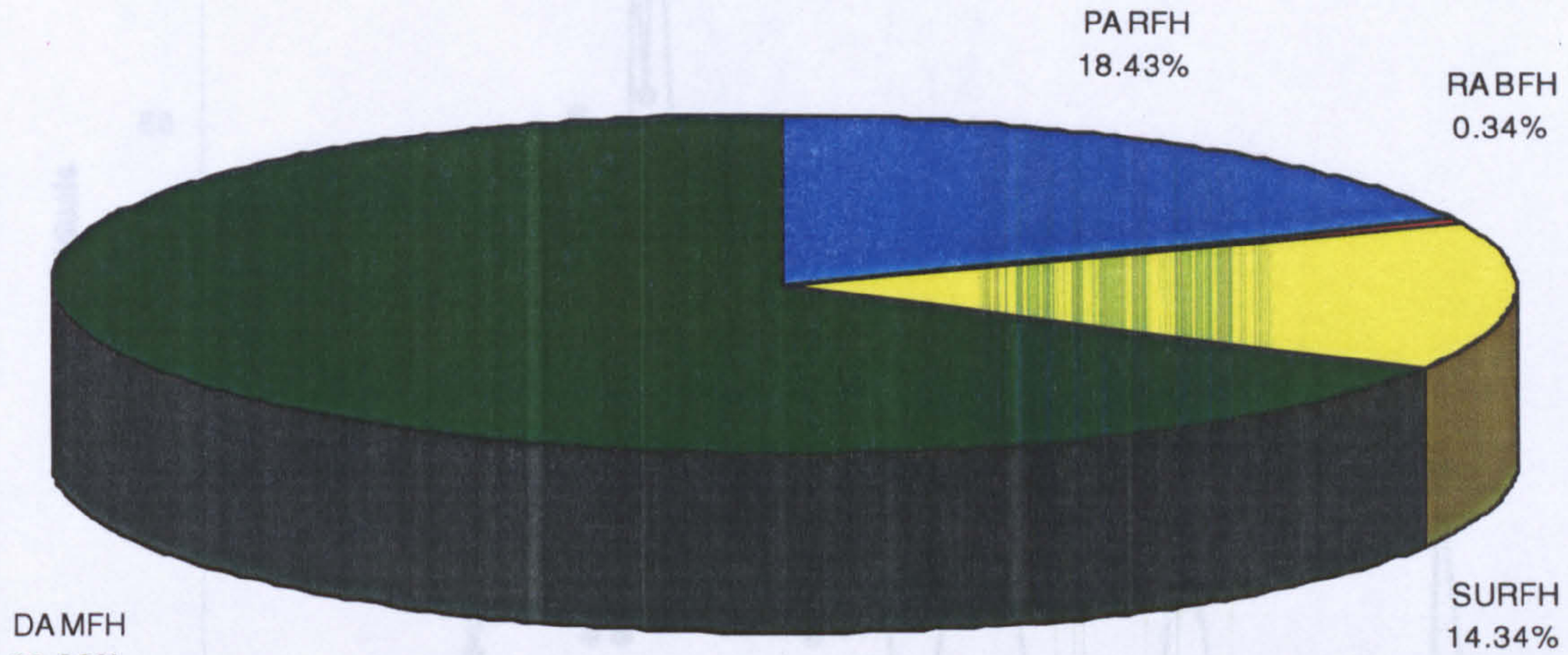


Figure 8.3: Composition of the **herbivorous fish** community at **Jana (deep)** based on average abundance recorded along the 50 m transect throughout the study period; PARFH = parrotfish, RABFH = rabbitfish, SURFH = surgeonfish, DAMFH = damselfish.

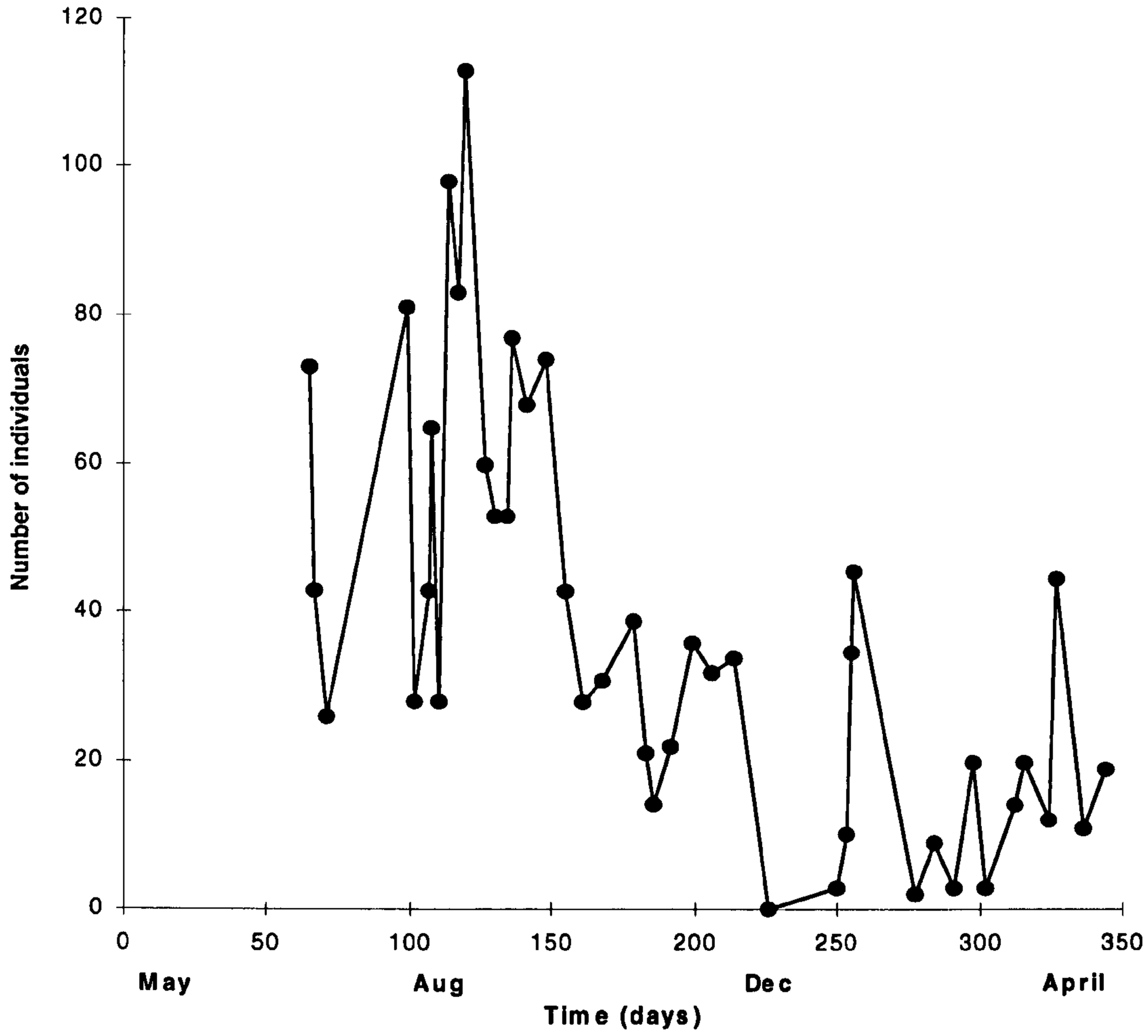


Figure 8.4: Abundance of *Siganus* **spp.** recorded along the 50 m transect at **Abu Ali**, throughout the study period.

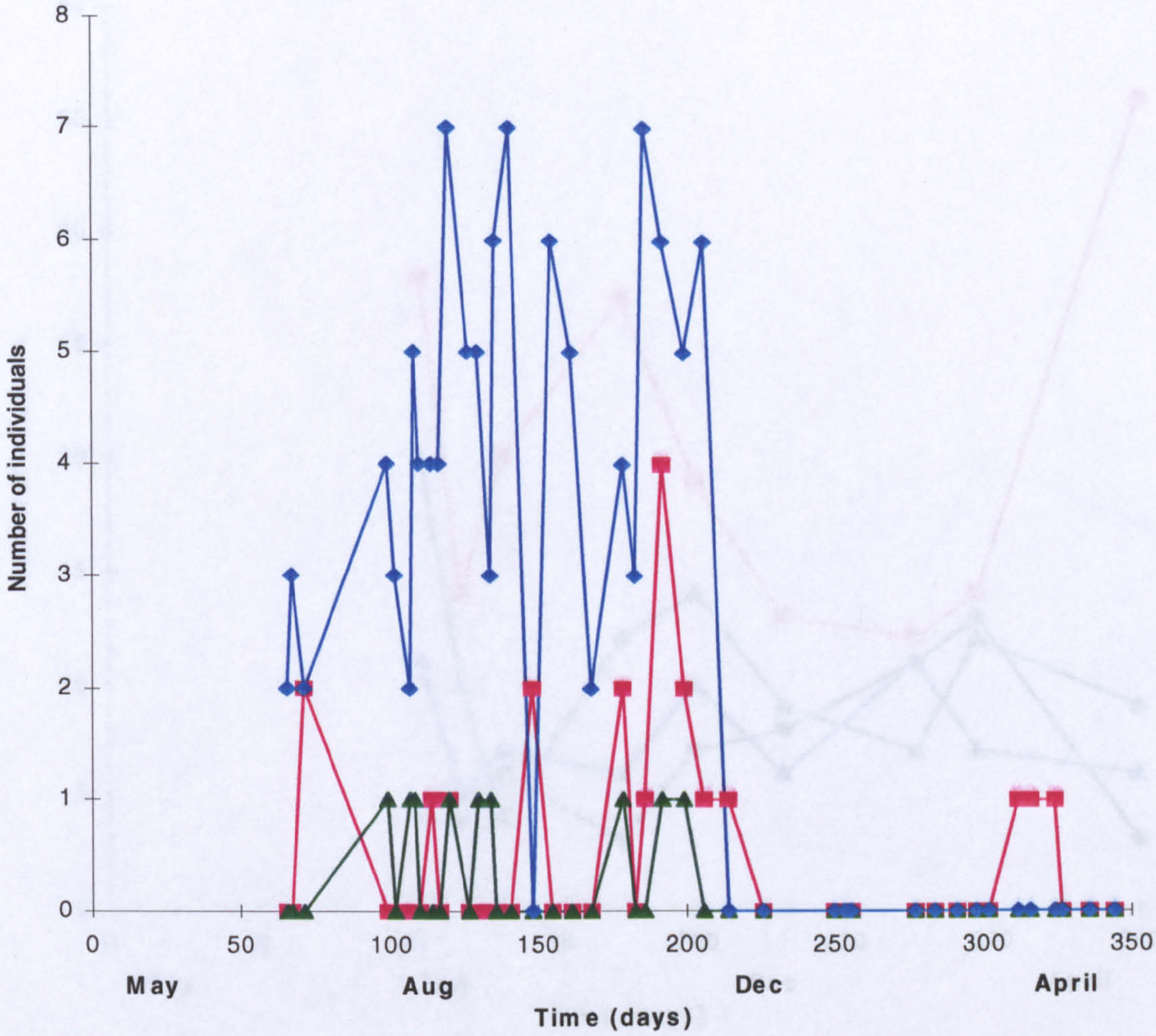


Figure 8.5: Abundance of **herbivorous fish** (other than *Siganus* spp.) recorded along the 50 m transect at **Abu Ali**, throughout the study period; (■) parrotfish, (▲) surgeonfish, (◆) damselfish.

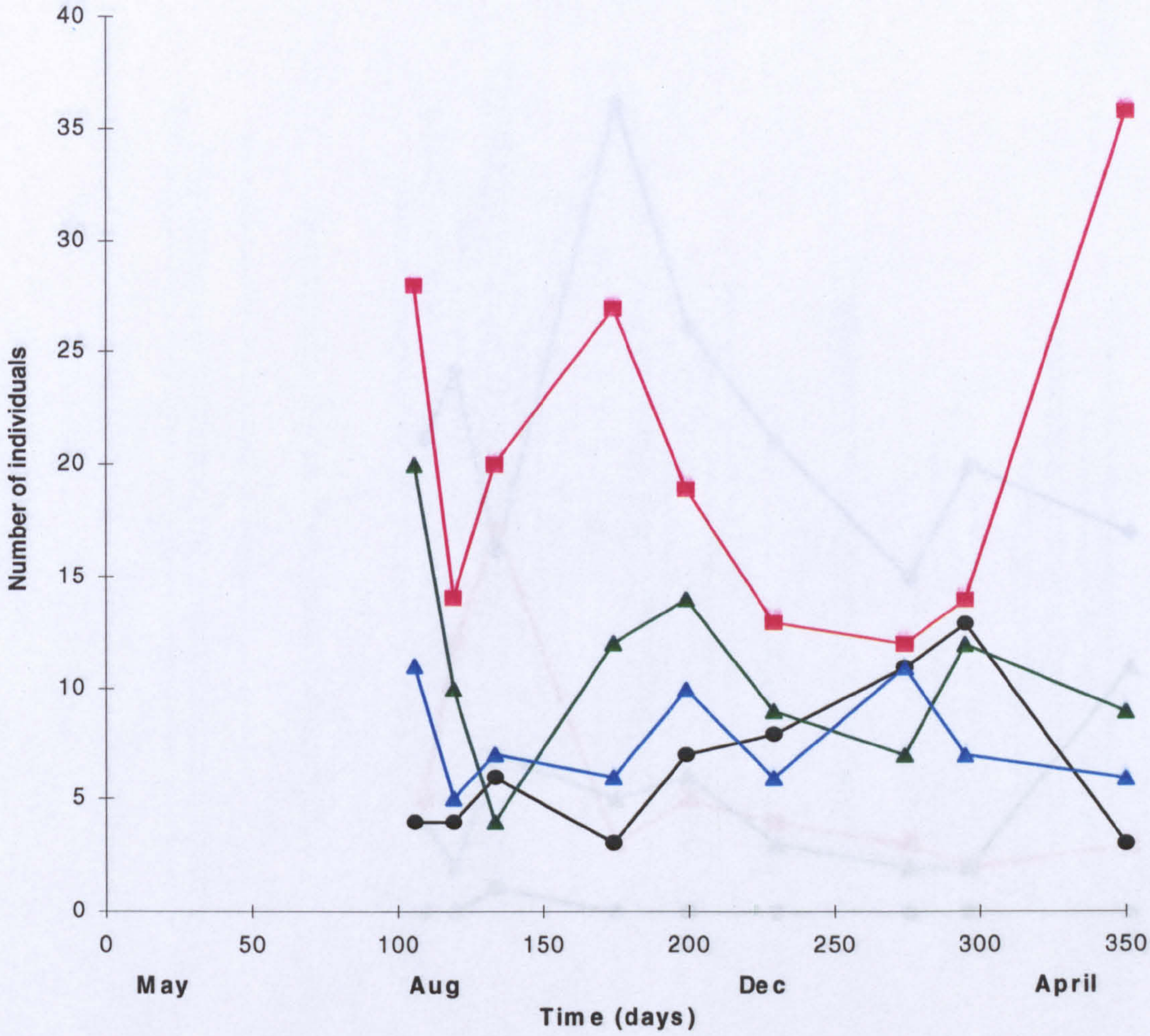


Figure 8.6: Abundance of **herbivorous fish** recorded along the 50 m transect at **Jana (shallow)**, throughout the study period; (■) parrotfish, (▲) surgeonfish, (◆) damselfish, (●) rabbitfish.

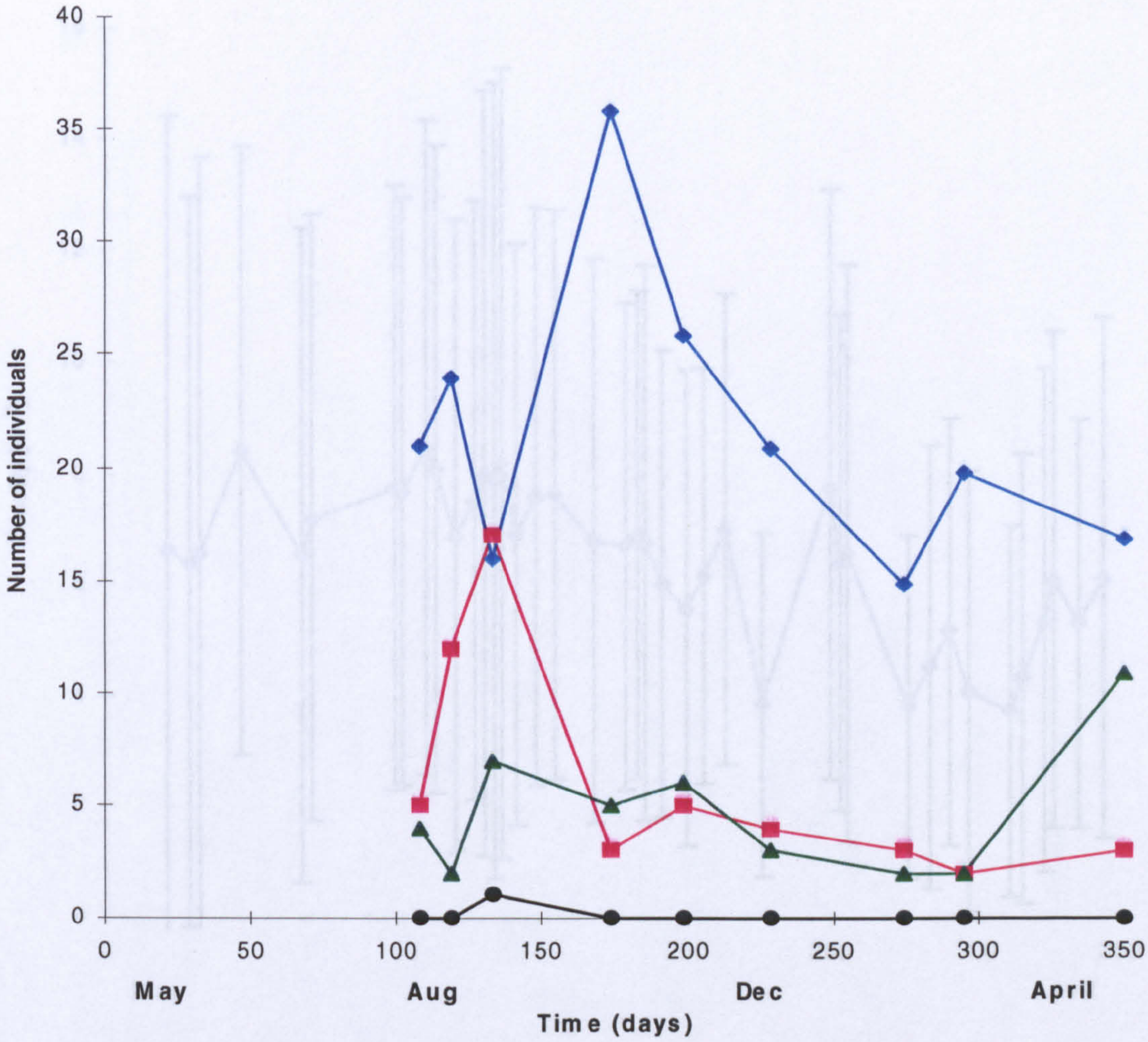


Figure 8.7: Abundance of **herbivorous fish** recorded along the 50 m transect at **Jana (deep)**, throughout the study period; (■) parrotfish, (▲) surgeonfish, (◆) damselfish, (●) rabbitfish.

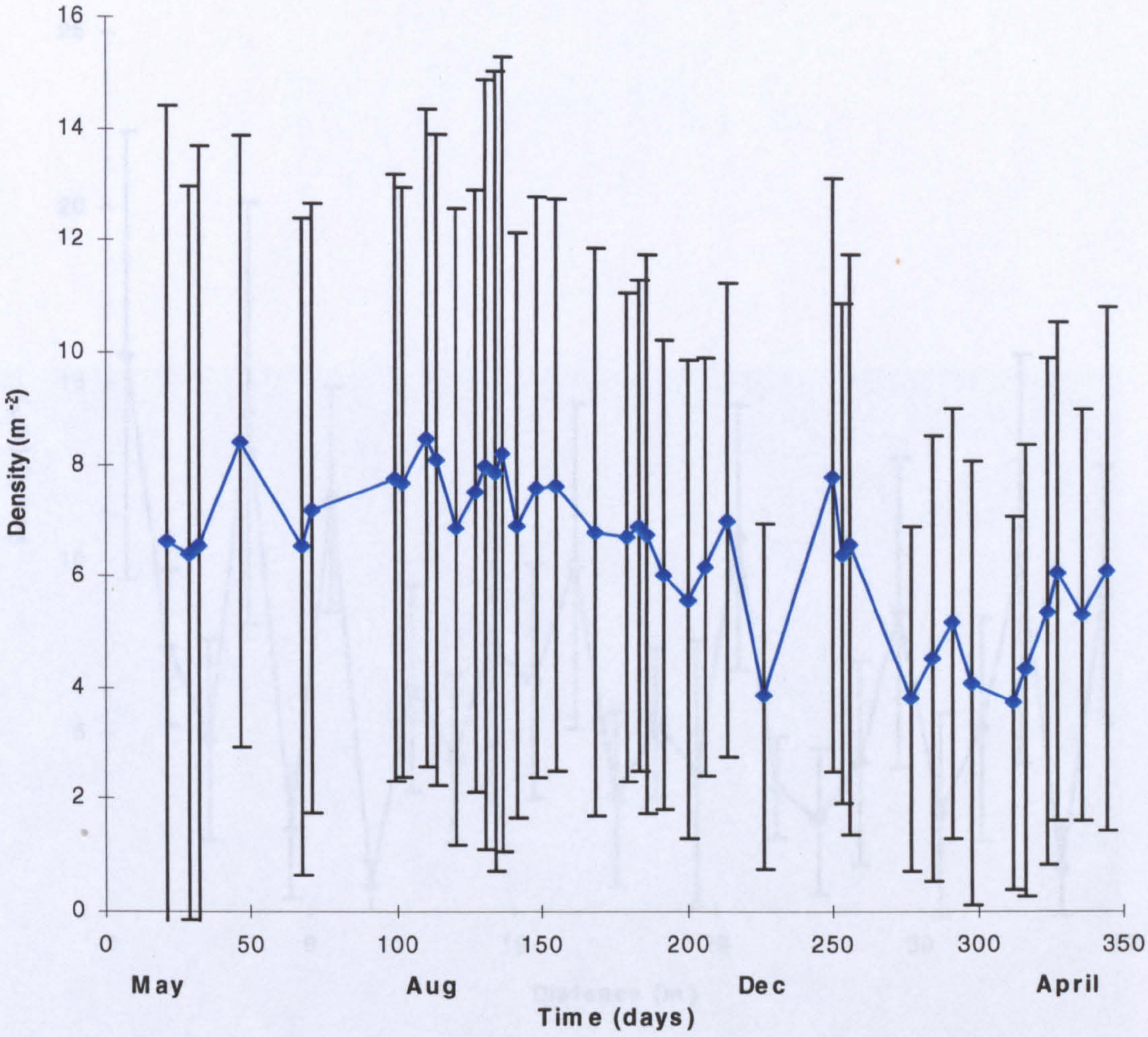


Figure 8.8: Mean density of ***E. mathaei*** ($x \pm$ SD, $n = 25$), recorded along the 50 m transect at **Abu Ali** throughout the study period.

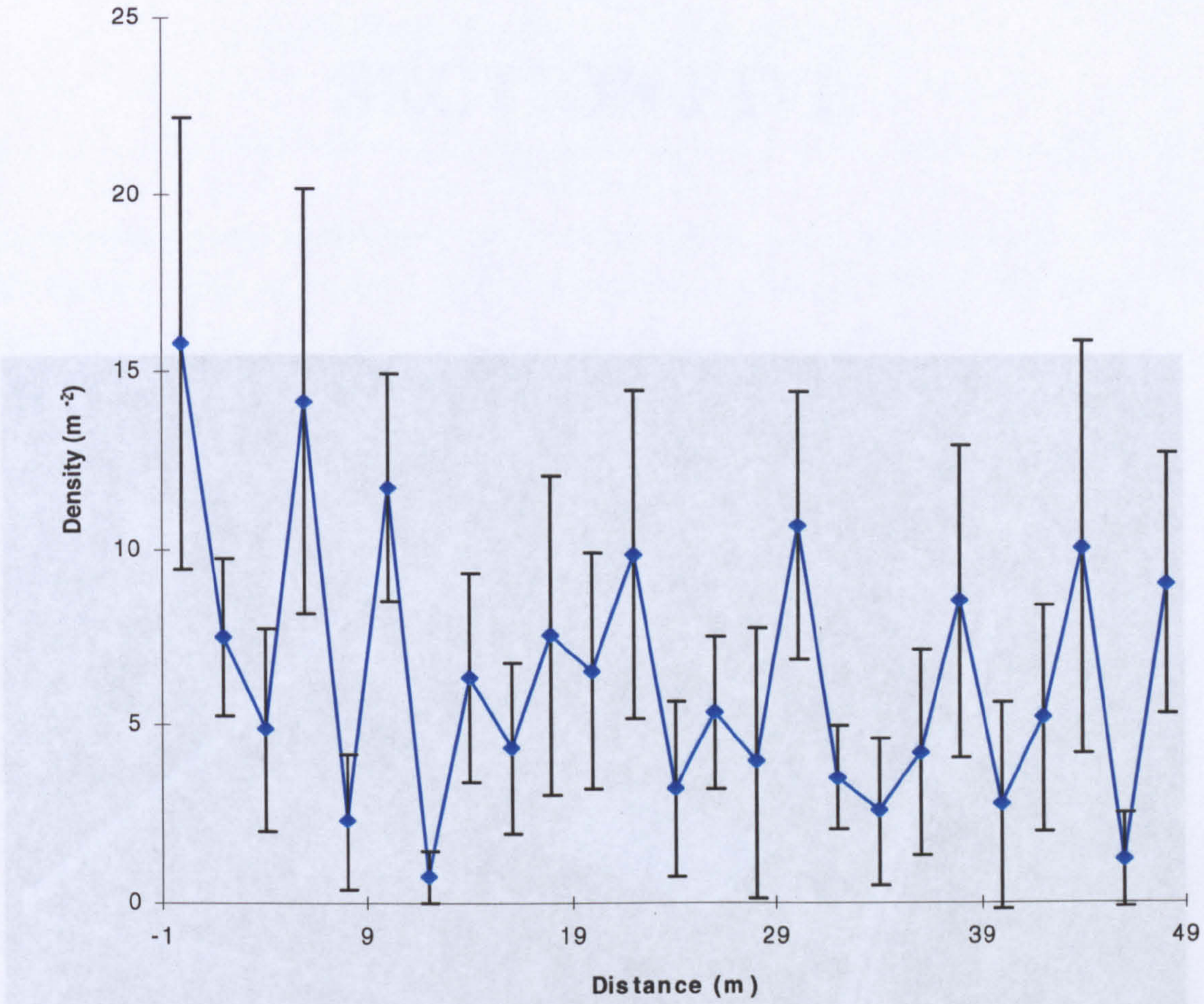


Figure 8.9: Mean density of ***E. mathaei*** ($x \pm$ SD, $n = 25$) per quadrat, recorded at the sampling stations along the 50 m transect at **Abu Ali**, throughout the study period.

SECTION FIVE

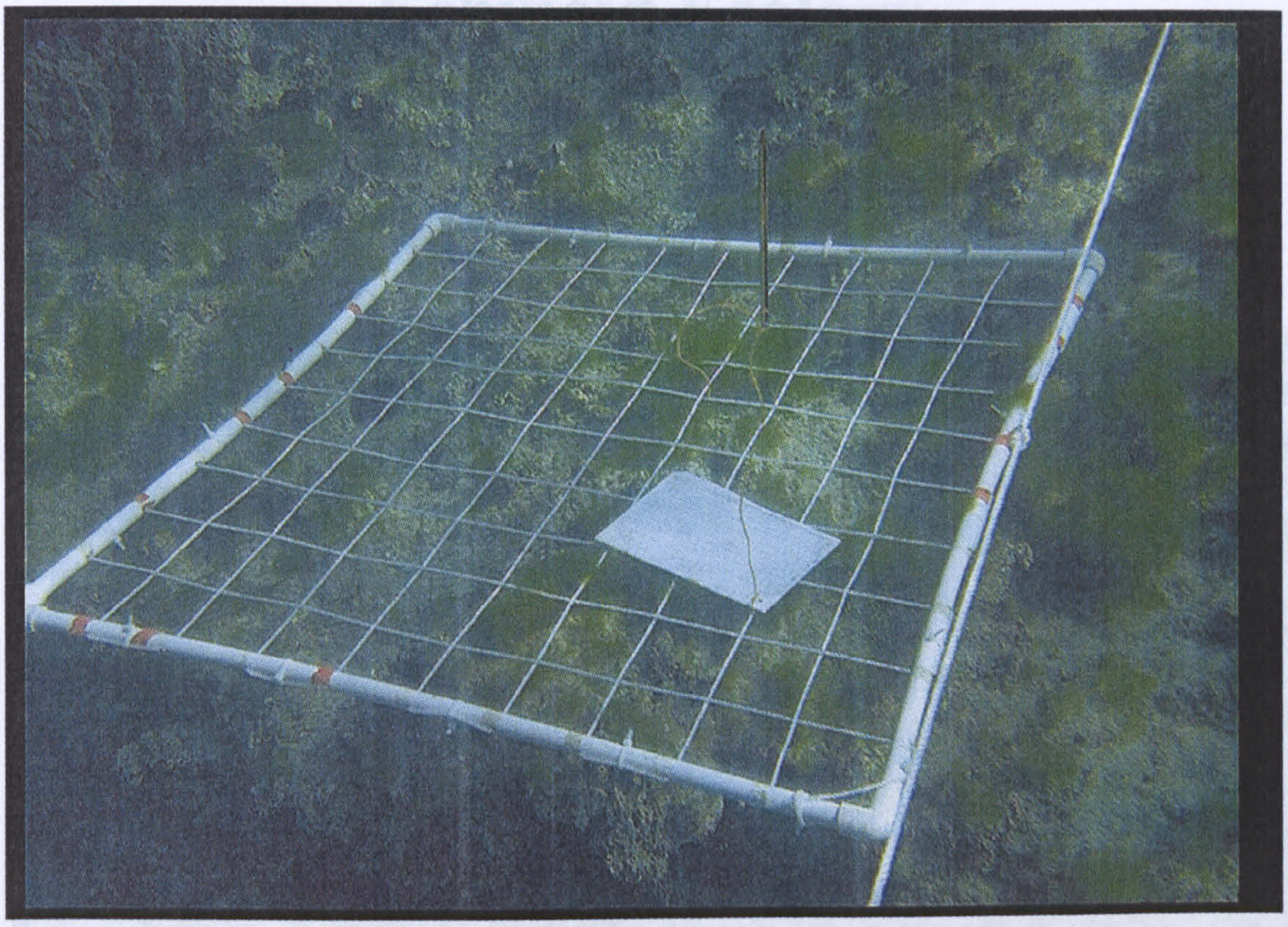


Plate 8.1: Section of the 50 m transect with 1 m^2 quadrat used to estimate the density of the *E. mathaei* population at Abu Ali (1/95).

SECTION FIVE

Echinoid Ecology

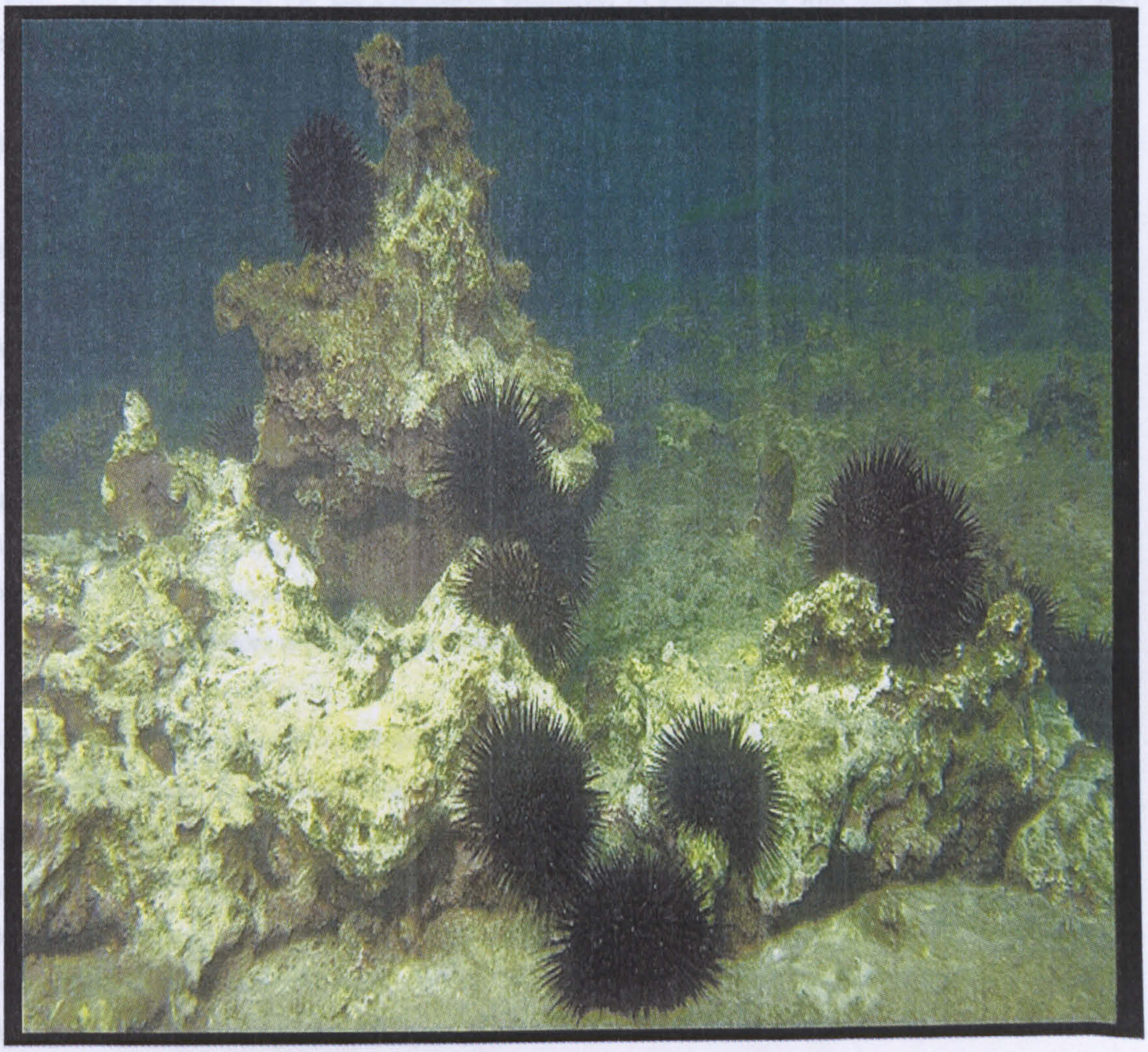


Plate 9.0: *Echinometra mathaei* at the inshore fringing reef at Abu Ali (8/94).

Chapter Nine

Grazing Rates and Bioerosion

Summary

The bioerosion rate of *Echinometra mathaei* (de Blainville) at the inshore fringing reef at Abu Ali was investigated using the gut evacuation technique described by Downing and El-Zahr (1987). There was no significant difference in evacuation rate between summer and winter, resulting in a mean bioerosion rate of 0.48 g urchin^{-1} day^{-1} or 3.15 g m^{-2} day^{-1}. However a seasonal difference in diel gut fullness was detected, probably reflecting an increase in grazing (gut filling) rate in response to increased food availability during the winter season. The results also suggest increased foraging activity during the day, and more sedentary nocturnal activity. Seasonal variations in sedimentation, and consequently the amount of reworked material ingested by *E. mathaei*, reduced the accuracy of the calculated bioerosion rates. The suitability of the gut evacuation technique, in comparison with other methodologies for estimating echinoid bioerosion, is discussed.

9.1 Introduction

It has long been established that grazing is an important process in the coral reef ecosystem with significant effects on reef growth, integrity and community structure (Hatcher, 1983; Steneck, 1988). Among the animal groups responsible, echinoderms are key players, primarily due to the bioerosive impacts resulting from their grazing, as well as burrow and crevice excavation activities (Hutchings, 1986). At moderate levels bioerosion is important for maintaining the reef integrity and colonising space (Sammarco, 1980; Birkeland and Randall, 1981; Sammarco, 1982b), but problems can arise when the erosion rate exceeds the reef growth rate and habitat degradation occurs (McClanahan and Muthiga, 1988). Previous increases in echinoid densities have been linked to several factors including a decline in fish predators resulting from overfishing (McClanahan and Shafir, 1990).

Various methods have been developed to quantify the rate at which reef substratum (i.e. calcium carbonate) is removed by a grazing echinoid. Lewis (1964) observed a gut turnover rate of 8-12 hours (i.e. 2.5 times per day) for *Diadema antillarum* and consequently proposed that the gut content weight (multiplied by 2.5) equates to a daily consumption rate. Hawkins and Lewis (1982), however, pointed out that if feeding behaviour is not continuous gut content weight should be considered only as an estimate of the minimum consumption over a 24-hour period. This concept has been applied in several studies and to different species (Glynn *et al.*, 1979; Scoffin *et al.*, 1980; Hawkins and Lewis, 1982; Bak, 1990). Hoskin and Reed (1985) argued that without verification of the gut turnover rate in each case, use of the minimum daily consumption estimate was unwise and instead proposed faecal pellet composition and defecation rate as an estimate of bioerosion.

On Kuwaiti offshore reefs in the Arabian Gulf, Downing and El-Zahr (1987) applied a similar approach to *Echinometra mathaei*, based on Russo's (1980) technique. However, instead of measuring faecal pellet production, defecation rate was indirectly estimated by monitoring the changes in gut content weight over a period of starvation. Furthermore, gut evacuation rate was shown to equal gut filling rate and was therefore considered to be an accurate estimate of bioerosion. McClanahan and Kurtis (1991) applied this gut evacuation technique to their studies of *E. mathaei* on Kenyan reefs.

The aim of the present study was three-fold: firstly to investigate diel changes in gut fullness of the *E. mathaei* population at the inshore study site; secondly to apply the gut evacuation technique to obtain overall and seasonal estimates of the bioerosive impact, and to make comparisons with other studies based on this approach (e.g. Kuwait: Downing and El-Zahr, 1987; Kenya: McClanahan and Kurtis, 1991). The final aim was to evaluate the proportion of calcium carbonate ($CaCO_3$) in the gut contents from the intake of recycled sediment and the grazed substratum.

9.2 Materials and Methods

9.2.1 Diel changes in gut fullness

Starting at dawn (i.e. time zero), 10 urchins were randomly taken from the reef every four hours over a 24-hour period and sacrificed. This experiment was conducted during both summer (August 1994) and winter (January 1995). Further details of the methods used and the physiological parameters measured are given in section 9.2.4.

9.2.2 Bioerosion

At time zero (i.e. dawn), 160 urchins were collected from the reef and distributed equally between two starvation cages located on the sandy backreef area immediately behind the fringing reef. This operation took no longer that fifteen minutes. The cages were 92 cm x 92 cm x 30 cm in size with double-meshed bases, and were raised approximately 15 cm above the substratum on aluminium stilts (Plate 9.1). The cages were weighted to the substratum by two diametrically opposed blocks and secured with the aid of plastic cable-ties (18 cm long and 5 mm wide). The experiment ran for a total of 54 hours, during which random samples of 10 urchins were taken at regular intervals from the cages and sacrificed. The sampling regime (in hours) employed after time zero was as follows: 0, 1, 2, 3, 5, 7, 9, 12, 16, 20, 24, 29, 34, 39, 44, 49, 54. This experiment was conducted during both summer (August 1994) and winter (January 1995). It is important to note that in the latter season only 100 urchins were starved for the first 24 hours of the sampling regime. Further details of the physiological parameters measured and the methods used are given in section 9.2.4.

Four different approaches were used to calculate the bioerosion rate of the inshore reef at Abu Ali. Method I applied the proportion of $CaCO_3$ in the gut (averaged from urchins sampled during diurnal feeding experiment) to the evacuation rate of dry gut content weight (Downing and El-Zahr, 1987). Method II used the results of measuring the evacuation rate of $CaCO_3$ directly (McClanahan and Kurtis, 1991), while Method III is based on minimum daily consumption and incorporated the average gut content weight of the urchins used in the diurnal feeding experiment (Bak, 1990). Method IV also used direct measurements of the $CaCO_3$ evacuation rate, but as a function of urchin test size.

9.2.3 Bioerosion vs. sedimentation

Twenty-five urchins were placed in a starvation cage, identical to those described in section 9.2.2, and starved for 5 days. During this time an additional 5 urchins were sacrificed in order to generate an estimate of the average gut fullness prior to starvation. After the starvation period 5 urchins were sacrificed to provide a baseline estimate of the average gut fullness at that time, while the remaining 20 urchins were equally distributed between two treatments. The first was the open reef substratum, and in order for the urchins to be retrieved at the end of the experiment some of the spines were coated with enamel paint. The second treatment was a pair of algal settlement panels (as described in section 5.2.1) onto each of which five urchins were placed and covered with an exclusion cage to prevent their escape (as described in section 6.2.1). These two treatments were left for 5 days after which all urchins were collected and sacrificed. The assumption behind this experiment was that the $CaCO_3$ content in the gut of a grazing urchin consists of two components: freshly eroded substratum material and reworked material ingested incidentally. In order to separate these two components the gut contents of urchins grazing on erodable (natural substratum) and non-erodable (settlement plates) material would be compared. Hence any difference in $CaCO_3$ content would be attributable to freshly eroded substratum material. This experiment was conducted during spring (April 1995). Further details of the physiological parameters measured and the methods used are given in section 9.2.4.

9.2.4 Sample preservation and analysis

For all experiments the sacrificed urchins were temporarily stored in 4% formalin solution (buffered with seawater) until they were taken to the laboratory and dissected. Due to the possibility of incomplete buffering and hence dissolution of $CaCO_3$ within urchin guts and tests, the diel feeding experiment was partially repeated using specimens stored in a neutral preservative (i.e. ethanol).

(a) Physiological measurements

For all urchins the following measurements were taken:

wet body weight
test diameter (long and short horizontal axes)
drained body weight
wet gut weight
wet gonad weight
wet Aristotle's Lantern weight

Test diameter was measured using Vernier callipers (to 0.1 mm) and wet weight using electronic balances (Sartorius *Basic*; to 0.01 g for body weights, and to 0.0001 g for internal organs). These parameters were used to produce estimates of gut fullness (% wet gut weight/ wet body weight ratio) and test size [(long axis + short axis)/2].

(b) Gut content analysis

After their removal, the complete guts and respective Aristotle's Lanterns were temporarily stored together in 70% alcohol. The $CaCO_3$ content was measured using a method developed by Downing and El-Zahr (1987) as follows:

Each gut sample was washed from its vial with distilled water onto a labelled, pre-weighed piece of hardened, ashless filter paper (Whatman No. 51). The gut tissue was dissected away, and the remaining contents were rinsed with distilled water using a suction filter. The samples were then transferred to a pre-heated oven and baked at 80 °C for 10 to 12 hours, after which they were placed in a desiccator to cool (for approximately 30 mins.) and then weighed (to 0.001 g). The samples were returned to the suction filter and soaked in 1 M HCl until the reaction with any $CaCO_3$ in the gut material was complete. After repeated rinses with distilled water, the samples were returned to the oven and again dried at 80 °C for 10 to 12 hours, cooled in the desiccator and re-weighed. Control pieces of filter paper were also used in the analysis in order to calculate the average loss in weight that each stage incurred. After these corrections were applied to the results, the difference in weight between the dried samples before and after the treatment with HCl was considered equal to the $CaCO_3$ content. In summary, the procedure generated an estimate of total dried gut content weight that was comprised of $CaCO_3$ and residual (mostly organic) content weights.

9.2.5 Data analysis

Statistical analysis of the data involved Model I ANOVA (2-way with replication) for all gut and physiological parameters, between season and time, for both diel gut fullness and gut evacuation experiments. Correlation and regression analysis was also employed to investigate linear temporal relationships. For the investigation of bioerosion versus sedimentation, ANOVA (1-way without replication) was performed.

9.3 Results

9.3.1 Diel changes in gut fullness

Gut fullness (% wet gut weight/ wet body weight ratio) for *E. mathaei* at Abu Ali did not vary significantly over 24 hrs during the summer and winter seasons (Figure 9.1; Table 9.1). The data were subsequently pooled to produce an average diel gut fullness of 5.00 ± 0.99 % and 8.78 ± 1.13 % (x ± SD, n = 60) for the respective seasons. (The proportion of gut fullness to drained body weight was 6.21% in summer and 10.24% in winter). Calcium carbonate content, the proportion of $CaCO_3$ in the gut (i.e. $CaCO_3$ weight/ dried gut contents weight ratio) and the residual content varied significantly over time (Table 9.1). In all cases the gut fullness, total weight and contents weight was significantly greater in winter than summer, while the converse was true for the proportion of $CaCO_3$ in the gut. However there was no significant diel difference for dried gut content weight. A comparison of the relative fractions of the dried gut contents over the 24-hour period between summer and winter can be seen in Figure 9.2.

Means of gut fullness, total dry and contents weights for each sampling period over 24 hours exhibited no significant diel change, except $CaCO_3$ weight during summer (Table 9.2). This is due to the larger amount of carbonate material detected during the last sampling period (i.e. 20 hours after sunrise; Figure 9.2). However, this significance is not borne out in the correlation analysis of the proportion of $CaCO_3$ in the gut ($CaCO_3$ / dried gut content; Table 9.2).

Gonad wet weight showed no significant seasonal or diel variation (ANOVA (2-way with replication), n = 120, $p > 0.1$ $p > 0.05$ respectively). However, there was a significant interaction term, ($p < 0.05$), indicating that summer gonad weight was slightly larger in the nocturnal period while winter gonad weight was larger during the diurnal period. While there was no significant size-dependent relationship between gut fullness (% wet gut weight/ wet body weight ratio) and test size in the summer season, a significant negative relationship was detected in the winter season (Table 9.2). Furthermore, a significant positive exponential relationship existed between dried gut content weight and test size, and $CaCO_3$ weight and test size, for both seasons (Table 9.2).

The $CaCO_3$ contents of the gut samples preserved in formalin solution were consistent with the subsample preserved in ethanol and it is assumed that the dilution of the formalin solution in seawater was sufficient to reduce the acidic properties to negligible levels.

9.3.2 Bioerosion rate

Changes in gut fullness (% wet gut weight/ wet body weight ratio) of *E. mathaei* over the starvation period for both summer and winter seasons are shown in Figure 9.3. Temporal differences in gut

weight during evacuation were not statistically significant, except for the residual content (Table 9.3). The total gut evacuation rate was calculated from a regression of the changes in gut weight, in terms of both complete wet gut weight and dry gut content weight (Figure 9.4). It is important to note that this is restricted to the first seven hours of starvation (i.e. when starvation is at a maximum (see Downing and El-Zahr, 1987; McClanahan and Kurtis, 1991). Similar calculations were made for the $CaCO_3$ evacuation rate in terms of actual weight and as a proportion of test size (Figure 9.5) Further statistical analysis (i.e. ANOVA) indicated that urchins in the winter season contained significantly more $CaCO_3$ in their guts than those in the summer. In addition, there was no significant short-term temporal change in the proportion of $CaCO_3$ in the guts, but again the ratio was significantly greater during summer (Figure 9.6; Table 9.3).

Incorporating the results of this experiment into the four different methods of calculating echinoid erosion rate (g $CaCO_3$ urchin^{-1} day^{-1}) produced a range of estimates (Tables 9.4 and 9.5). Method I generated summer and winter erosion rates of 0.736 and 0.548 g urchin^{-1} day^{-1} respectively, while Method II estimated them as 0.528 and 0.348 g urchin^{-1} day^{-1} respectively. Furthermore the summer and winter estimates by Methods III and IV were 0.537 and 0.904 g urchin^{-1} day^{-1}, and 0.490 and 0.479 g urchin^{-1} day^{-1} respectively.

9.3.3 Bioerosion vs. sedimentation

The previous level of gut fullness was re-attained by all sampled individuals as there was no significant difference between those urchins before starvation (i.e. gut evacuation) and those after a period of foraging (i.e. gut filling), on either natural reef substratum or artificial settlement plates (ANOVA (1-way), $n = 21$, $p > 0.10$). However, the $CaCO_3$ weight in the gut contents sampled after a period of foraging was significantly larger than those before starvation (ANOVA (1-way), $n = 19$, $0.01 < p < 0.05$). Although starvation for five days produced a 25 % reduction in $CaCO_3$ weight, subsequent foraging resulted in a five-fold increase (Table 9.6). Furthermore, comparisons of the means revealed no significant difference between the two treatments (t-test $p = 0.05$). A significant difference was also detected in the percentage of $CaCO_3$ in the gut contents (ANOVA (1-way), $n = 19$, $0.01 < p < 0.05$), but comparison of means revealed that the only non-significant relationship was between those urchins before starvation and those that foraged on the settlement plates (t-test $p = 0.05$).

9.3.4 Urchin test size

There was no significant difference in test size of the urchins sampled throughout the diel feeding experiment, either over the short-term or between seasons (Figure 9.7; Table 9.7). Correlation analysis of the separate seasonal data sets also revealed a non-significant temporal relationship ($r = 0.68$, $n = 6$, $p = > 0.1$) and ($r = -0.77$, $n = 6$, $p = > 0.05$) for summer and winter respectively. Similarly for the urchins sampled during the evacuation experiment, neither the difference in test size between seasons

nor the interaction term was significant (Figure 9.7; Table 9.7). Again, correlation analysis revealed a non-significant temporal relationship for both seasons ((r = -0.80, n = 6 , p = > 0.05) and (r = 0.50, n = 6 , p = > 0.1) for summer and winter respectively).

Test size data from the diurnal feeding experiment was pooled for both summer and winter (due to the non-significant relationship over the twenty-four hour period) to produce a mean test size of 51.05 ± 4.17 mm (x ± SD, n = 57) for summer and 49.89 ± 5.59 mm (x ± SD, n = 60) for winter. The pooled test size frequency data showed an apparently 'normal' distribution (Figure 9.8). The non-significant relationship between seasons was considered as reasonable justification to pool these two averages to produce an overall average test of 50.45 ± 4.97 mm (x ± SD, n = 117). Due to possible influences of starvation on test size the data from the evacuation experiment was not pooled in this manner.

9.4 Discussion

9.4.1 Diel feeding

Gut fullness did not vary significantly either diurnally or nocturnally. Downing and El-Zahr (1987) also found no difference in the diurnal gut fullness of *E. mathaei* from Kuwaiti offshore reefs and concluded that feeding rate continued at an equal rate. However this assertion only implies that the urchins' gut filling and evacuation rates are equal; it does not reveal whether this balanced feeding rate changes pace or even stops, at any time.

Relative proportions of the gut constituents did, however, vary significantly over the entire diurnal and nocturnal period. For example, in both seasons the residual content (mainly organic material), increased during the day, reached a maximum by sunset, and decreased again throughout the night (Figure 9.2). The reverse was true for the $CaCO_3$ content during the winter season, while in the summer it increased consistently, attaining a maximum during the nocturnal period. Two factors may be solely or partly responsible for the observed temporal differences. Firstly, that the relative proportions of the gut contents are simply indicative of the quality of habitat being grazed, and therefore merely reflect the abundance of the resources available. Secondly, urchins may exhibit selective feeding behaviour. The fact that an increase in residual content is observed during both seasons despite the significant differences in resource availability (see Chapter Five), supports the idea of selective feeding behaviour. In their study, Downing and El-Zahr (1987) also suggested that a difference in the proportion of $CaCO_3$ in the gut (a decrease of 3%) was possibly evidence for a variation in feeding behaviour over the diurnal period. Unfortunately data from the present study do not enable determination of the relative importance of the two factors.

Whether this selective behaviour is based upon activity and feeding rate or food detection is also unclear. If feeding activity alone was responsible then the relative proportions of the gut contents might

not be expected to change, but since it has been statistically proven that they do, then an element of resource selectivity while feeding could be inferred. Again, however, the data from the present study cannot be used to determine the relative significance of the two factors (see also Chapter 10).

While the bias of resource preference is probable, changes in feeding activity alone can account for the observed results. For example, the fact that the overall gut weight does not change means that whether feeding is continuous or intermittent, gut filling and evacuation processes are not independent. If feeding did cease for an extended period then the gut contents should remain unchanged during that time. This is not evident in the results, although the data are based on averages sampled from several individuals over time and not continuously from one individual. Furthermore, the sampling regime may have been too infrequent. However the fact that gut contents significantly change throughout the entire diel period would suggest continuous feeding; changes in rate are not relevant, only that gut filling and evacuation processes are equal (but see 9.4.3 below).

Assuming that feeding is probably continuous, the increased residual gut content during the diurnal period strongly suggests that the urchins are grazing the substratum selectively and/or more actively during the daytime. There is no direct evidence in the present study to confirm or deny substratum selectivity, but the latter would be in accordance with the observed results. By foraging over a wider area during the diurnal period urchins can graze larger areas of substratum, perhaps selectively, and can thereby increase the organic content relative to $CaCO_3$ material ingested during grazing. However, during the nocturnal period the urchins are more sedentary, maybe even returning to particular crevices, over-grazing a smaller area and consequently ingesting proportionally larger quantities of $CaCO_3$ material.

Particularly striking is that urchins sampled during winter consistently contained more $CaCO_3$ material than those from the summer, although the summer season maintained a significantly larger proportion of $CaCO_3$. Conversely winter urchins contained a larger amount of organic and other residual material than urchins sampled during summer. As an urchin's test has a finite volume, it was initially assumed that this result was an artefact due to a difference in the reproductive state and therefore gonad ripeness (i.e. those in the summer were sampled during a more advanced, enlarged stage). However, statistical comparison of wet gonad weight between the two seasons has shown that this is not the case. Hence the difference in gut fullness is either due to variations in feeding behaviour and/or environmental conditions which are discussed below.

9.4.2 Bioerosion rate

While of similar magnitude, the erosion rates produced by the different methods (Tables 4 and 5) would, if considered in isolation, lead to conflicting conclusions about the bioerosive impact of *E. mathaei*. For example, Method I and II indicate that the winter season supports a slower erosion rate,

as both approaches are based upon the evacuation rates of actual gut component weights (e.g., in which winter results consistently showed a slower rate). Furthermore, Method I has a lower level of resolution and accuracy as its calculations incorporate the total dried gut content evacuation rate and averages from the diurnal feeding experiment (i.e. % $CaCO_3$ content). Method II however, relies solely on the direct measurement of the $CaCO_3$ evacuation rate.

In contrast, Method III produces the opposite trend in seasonal bioerosion rate; the summer supports the slower rate. This approach is based on an estimate of the average $CaCO_3$ content of the gut in any diurnal period, assuming that an urchin completely evacuates its gut contents in a 24-hour period (Lewis, 1964). While this may be true for *D. antillarum*, it is clear from the gut fullness data during the evacuation experiment that *E. mathaei* had not completely evacuated its guts during the first 24 hours, particularly in the winter season. Hence the erosion rates produced by Method III are gross overestimates and must be discarded.

Of the above estimates discussed so far, those produced by Method II would appear to be the most accurate. However, there is probably some inaccuracy, as the method considers the evacuation rate of actual $CaCO_3$ weight in the gut and does not account for any effects of urchin size. It has been shown in this and other studies (Scoffin *et al.*, 1980; Bak, 1990) that gut content increase exponentially with test size. Consequently, estimating the evacuation rates based on actual gut weights assumes that the test sizes of the sampled urchins are not significantly different. Any difference will influence the slope of the regression line used to calculate the overall rate. In this study, the test size of the urchins sampled did not vary significantly over time during either season. However, urchins have been shown to undergo negative growth in response to starvation or food-limiting conditions (Levitan, 1988b,1989,1991a). This response has only been observed in *D. antillarum* and only after long periods of food-limitation (i.e. > 24 hours). *E. mathaei* is probably affected little by this phenomenon (McClanahan and Kurtis, 1991). But in order to eliminate any possible sampling bias, the evacuation rate is calculated as a ratio of $CaCO_3$ weight and test size (Figure 9.5), resulting in the erosion rates produced by Method IV. Here, there is no longer any seasonal difference in evacuation rate and using the pooled average test size of the urchins sampled during the diurnal feeding experiment, produces a population erosion rate of 0.48 g urchin^{-1} day^{-1}. This figure, in combination with the average population size estimated for the inshore reef (Chapter 8), generates a surface area erosion rate of 3.15 g m^{-2} day^{-1}.

McClanahan and Kurtis (1991) using the same evacuation technique while working on Kenyan reefs, estimated a comparable erosion rate of 0.42 g urchin^{-1} day^{-1} for *E. mathaei* on Kenyan reefs (using Method II described above). Downing and El-Zahr (1987) working with *E. mathaei* on Kuwaiti reefs calculated a significantly greater erosion rate of 1.4 g urchin^{-1} day^{-1} (Method I). However, this increase is attributed to the higher population density (30 m^{-2}) and the positive relationship between the proportion of $CaCO_3$ in the gut and population density (McClanahan and Kurtis, 1991).

9.4.3 Effect of seasonality

One very important result from this study still remains unexplained: the significant seasonal difference in gut fullness for both $CaCO_3$ and residual (i.e. primarily organic) content. Based on the findings of Downing and El-Zahr (1987) (see section 9.4.1 above), gut filling equals gut evacuation rate, but with the fundamental assumption that the urchin guts are being filled to full capacity. The seasonal difference in gut fullness revealed in this study refutes this assumption. Furthermore, if there is no difference in seasonal gut evacuation rate (from Method IV) and gut filling equals gut evacuation rate then a seasonal difference in gut fullness should not occur. Thus the idea of a balanced filling and evacuation rate does not hold for all seasons. Intuitively, a seasonal difference in gut evacuation rate might be expected due to the considerable seasonal differences in temperature (Coles, 1988; Chapter 4) and food availability (e.g., macroalgae; Coles 1988; Chapter 5). For example, if gut evacuation is an indirect measure of digestion rate, the influence of lower winter temperatures on metabolism and the time taken to digest a more nutrient rich diet might suggest a slower evacuation rate for the winter months (as described in Method II; Figure 9.5). Instead, the results suggest that either digestion is not influenced by these environmental changes, or that digestion is not linked to evacuation rate, the latter being a purely mechanical process occurring continuously throughout the year. However, given that evacuation rates are equal between seasons then the difference in gut fullness must be caused by an increased filling rate during the winter. The assumption here is that evacuation rate is operating at its maximum.

The conclusion, however, that gut filling does not always equal gut evacuation rate, particularly in the winter, contradicts the conclusions made in section 9.4.1. The fact that there was no significant difference in gut fullness over time would not now imply a balanced filling and evacuation rate, but simply that the difference in the two rates is not large enough to produce a measurable change over 24 hours. To test these predictions would require a gut filling experiment whereby the increase in gut fullness of starved individuals is measured over time (Downing and El-Zahr, 1987). For example, it may be that only during the summer months does gut filling rate equal the gut evacuation rate. Either way, the gut fullness results during the summer suggest that a combination of gut filling, digestion and evacuation rate are maintaining gut fullness below maximum capacity.

Also important is that the process of gut filling comprises two elements. Firstly, the rate at which the substratum is grazed (i.e. the number of bites taken over time) and, secondly, the volumetric size of the mouthfuls consumed with each bite. The conclusion therefore that during the summer season there is a slower gut filling rate, can be explained as follows.

Food availability varies considerably throughout the year. In summer, the reef substratum is characterised by a simple covering of filamentous epilithic algae while in the winter it includes a large

standing crop of macroalgae (Coles, 1988; Chapter 5). During summer the urchins will be forced to actively graze and erode the substratum in order to ingest any nutritious material. During winter the abundance of algae covering the substratum would ensure larger mouthfuls were ingested per bite which would require less expenditure of energy. Hence, gut fullness would be expected to increase throughout the winter months. Any seasonal difference in bite rate would reflect a trade-off between an increased response to food-limiting conditions in summer and the counteracting increase in the winter due to a reduction in physical effort required to graze the substratum.

While increased food availability can explain the higher gut filling rate and therefore the higher residual (primarily) organic gut content in winter (e.g. over 250% greater than summer), it does not explain the observed seasonal increase (e.g. approximately 50 %) in $CaCO_3$ content. For example, the inference that with increased food availability less effort is needed to graze the substratum would result in a lower $CaCO_3$ content in the gut in winter than in summer. Urchins in summer proportionally contain more $CaCO_3$ than in winter, as might be expected in a food-limited situation where individuals are subsequently forced to graze the substratum more actively. But in terms of actual weight the urchins in the winter contain more substratum material. A possible source of easily ingestable $CaCO_3$ material would be a seasonally increased sediment deposition rate. The winter season along the Saudi Arabian Gulf coast is characterised by strong winds and increased turbidity (Chapter 4). At the inshore reefs, in particular, this will result in an increased rate of sediment movement and deposition. The hypothesis therefore is that higher levels of sedimentation aided by entrapment amongst the large standing crops of macroalgae, results in an increased ingestion of $CaCO_3$ material by the grazing urchins.

Hence the $CaCO_3$ material contained in the urchin guts from the winter cannot be considered as entirely freshly eroded material. This of course has important implications for the estimates of the erosion rates as they will all conceivably be overestimates, particularly in winter.

9.4.3 Effect of sedimentation

The results in section 9.2.3 imply that all of the $CaCO_3$ material ingested by urchins on the natural substratum was entirely reworked material, suggesting very limited bioerosion during winter. This conclusion is supported by the fact that the weight of $CaCO_3$ in the gut after filling, on either natural substratum or settlement plate, was comparable to the winter estimate of the average diel gut fullness (Table 9.1).

However several factors may have influenced the results. Most significant is the large discrepancy observed between the gut contents of the pre-starved urchins and those from the natural substratum treatment, as these should have intuitively been the same. An obvious explanation is a difference between the sample area of the reef and the treatment area. The urchins prior to starvation were randomly sampled from the reef study site, while the urchins after treatment were placed in one area

suitable for their recapture. The pre-starved urchins contained far more residual material in their guts and must have therefore, on average, been sampled from areas with a higher macroalgal cover, while the treatment area was significantly devoid of macroalgae. In addition, the design of the exclusion cages and settlement plates may have exacerbated the level of sedimentation (see Chapter 5) and therefore the potential for ingestion. Furthermore, the very small sample sizes of the data sets, for pre-starved urchins in particular, means that the results often contain a high variance. While it may not be possible to accurately quantify the proportion of reworked material in the guts of *E. mathaei* at the inshore fringing reef at Abu Ali, it is evident that reworked material contributes significantly to the overall gut content, particularly during winter.

Other studies have estimated the proportion of reworked material ingested by examining thin sections of faecal pellets and identifying the reworked sediment grains from amongst the faecal particles. Scoffin *et al.*, (1980) found that pellets of *D. antillarum* contained 10-68 % reworked material which was positively correlated with test size. Bak (1990), working with *D. savignyi* and *Echinothrix diadema*, found proportions of 33 % and 48 % respectively. *E. mathaei* was included in the latter study, but proportions of reworked material were not given.

Hoskin and Reed (1985) suggest an alternative method of estimating erosion rates which excludes the problem of ingested reworked sediment. In their study of *E. lucunter*, rocks containing a burrow and its resident urchin were carefully excavated from the reef and enclosed in a submerged bucket. Consequently, contamination by sediment from outside sources is minimised and all sediment produced by the urchin is captured whether ingested or not (i.e. spine abrasion). The possible disadvantages of this method include the exclusion of drifting food material, such as algal detritus, and the influence of reduced water flow inside the bucket.

9.4.4 Conclusions

Having determined that gut filling rate is equivalent to gut evacuation rate, the gut evacuation method was proposed by Downing and El-Zahr (1987) as a technique for measuring the erosion rate by *E. mathaei* in view of its simplicity. However this study has shown that this relationship does not always hold, but this limitation may only apply to urchin populations on reefs that undergo significant seasonal changes, such as the inshore reefs along the Arabian Gulf coast. However the gut evacuation technique does not incorporate any estimate for the proportion of re-worked material in the gut contents. Hence any rates of bioerosion calculated by this method are based on the total $CaCO_3$ content in the gut and will therefore be overestimates. Furthermore, the proportion of reworked material in the guts, and inversely the level of bioerosion that is occurring, will fluctuate in areas where there is a seasonal variation in sedimentation rates and macroalgal abundance.

In summary, use of gut evacuation or defecation rates would seem a valid estimate of bioerosion. It is a measure of the amount of $CaCO_3$ material ingested during grazing, not simply a direct measure of the intake rate. However, it is recommended that any estimate of echinoid bioerosion should incorporate measurements from different seasons before any overall estimate for annual reef erosion by echinoid grazing can be extrapolated.

	ANOVA (2-way with replication)			Mean ± 95% Confidence limits (SD in parentheses)		
	n	Season	Time	*n*	Summer	Winter
Gut fullness (% WG/WB wt)	120	S $p < 0.001$	NS $p > 0.5$	60	5.00 ± 0.26 (0.99)	8.78 ± 0.29 (1.13)
Dried gut contents (g)	120	S $p < 0.001$	NS $p > 0.1$	60	0.99 ± 0.10 (0.39)	2.11 ± 0.16 (0.62)
$CaCO_3$ content (g)	118	S* $p < 0.001$	S* $p < 0.001$	59	0.53 ± 0.07 (0.28)	0.90 ± 0.08 (0.31)
$CaCO_3$ content ($CaCO_3$/DGC wt)	118	S* $p < 0.001$	S* $p < 0.001$	59	0.53 ± 0.05 (0.17)	0.44 ± 0.04 (0.13)
Residual content (g)	118	S $p < 0.001$	S $p < 0.001$	59	0.46 ± 0.07 (0.27)	1.20 ± 0.13 (0.50)

Table 9.1: **ANOVA** results of the **diel feeding experiment** for gut fullness (% wet gut / wet body weight), dried gut content weight (DGC), $CaCO_3$ weight, proportion of $CaCO_3$ ($CaCO_3$ / DGC) in the gut and residual content weight. Means with 95 % confidence limits are also given. S = significant, NS = non-significant, SD = standard deviation. An asterisk (*) denotes a significant interaction term.

	Correlation Analysis			
	n	**Summer**	***n***	**Winter**
Gut fullness (% WG/WB wt)	6	NS $p > 0.1$, $r = 0.67$	6	NS $p > 0.1$, $r = -0.53$
Dried gut contents (g)	6	NS $p > 0.1$, $r = 0.62$	6	NS $p > 0.5$, $r = -0.05$
$CaCO_3$ content (g)	6	S $p < 0.05$, $r = 0.91$	6	NS $p > 0.5$, $r = 0.12$
$CaCO_3$ content ($CaCO_3$/DGC wt)	6	NS $p > 0.05$, $r = 0.74$	6	NS $p > 0.1$, $r = 0.46$
Residual content (g)	6	NS $p > 0.1$, $r = -0.37$	6	NS $p > 0.1$, $r = -0.49$
Gut fullness vs. Test size	60	NS $p > 0.1$, $r = 0.09$	60	S $p < 0.05$, $r = -0.28$
Log (dried gut content) vs. Log (Test size)	57	S $p < 0.001$, $r = 0.43$	60	S $p < 0.001$, $r = 0.77$
Log ($CaCO_3$) vs. Log (Test size)	56	S $p < 0.01$, $r = 0.38$	59	S $p < 0.001$, $r = 0.57$

Table 9.2: **Correlation analysis** of the **diel feeding experiment** for gut fullness (% wet gut / wet body weight), dried gut content weight, $CaCO_3$ weight, proportion of $CaCO_3$ ($CaCO_3$ / DGC) in the gut, residual content weight. In addition, gut fullness (% wet gut / wet body weight), dried gut content weight and $CaCO_3$ weight against test size. S = significant, NS = non-significant.

	ANOVA (2-way with replication)			Correlation Analysis		
	n	Season	Time	*n*	Summer	Winter
Wet gut weight (g)	120	S $p < 0.001$	NS $p > 0.1$	6	S $p < 0.01$ $r = -0.97$	S $p < 0.05$ $r = -0.88$
Dried gut contents (g)	120	S $p < 0.001$	NS $p > 0.05$	6	S $p < 0.05$ $r = -0.84$	S $p < 0.05$ $r = -0.88$
$CaCO_3$ content (g)	119	S $p < 0.001$	NS $p > 0.1$	6	S $p < 0.05$ $r = -0.85$	NS $p > 0.1$ $r = -0.53$
$CaCO_3$ content ($CaCO_3$/DGC wt)	119	S $p < 0.001$	NS $p > 0.1$	6	NS $p > 0.1$ $r = 0.50$	NS $p > 0.5$ $r = 0.22$
Residual content (g)	118	S $p < 0.001$	S $p < 0.05$	6	NS $p > 0.1$ $r = -0.66$	S $p < 0.05$ $r = -0.88$
Ratio of $CaCO_3$/Test size	118	S $p < 0.001$	NS $p > 0.1$	6	S $p < 0.05$ $r = -0.86$	NS $p > 0.1$ $r = 0.55$

Table 9.3: **ANOVA** and **correlation analysis** results of the **gut evacuation experiment** for wet gut weight, dried gut content weight (DGC), $CaCO_3$ weight, proportion of $CaCO_3$ ($CaCO_3$ / DGC) in the gut, residual content weight and the ratio of $CaCO_3$ weight to test size. (The interaction term was non-significant in all cases). S = significant, NS = non-significant.

(a)

Season	Evacuation Rate: Dried gut contents (g urchin^{-1} hr^{-1})	Evacuation Rate: Dried gut contents (g urchin^{-1} day^{-1})	Mean % proportion of $CaCO_3$ in dried gut contents	Erosion Rate: $CaCO_3$ (g urchin^{-1} day^{-1})	Population size (m^{-2})	Erosion Rate: $CaCO_3$ (g m^{-2} day^{-1})
Summer	0.058	1.392	52.885	0.736	6.5	4.78
Winter	0.052	1.246	43.999	0.548		3.56

(b)

Season	Evacuation Rate: $CaCO_3$ (g urchin^{-1} hr^{-1})	Evacuation Rate: $CaCO_3$ (g urchin^{-1} day^{-1})	Mean % proportion of $CaCO_3$ in dried gut contents	Erosion Rate: $CaCO_3$ (g urchin^{-1} day^{-1})	Population size (m^{-2})	Erosion Rate: $CaCO_3$ (g m^{-2} day^{-1})
Summer	0.022	0.528	n/a	0.528	6.5	3.43
Winter	0.016	0.348	n/a	0.348		2.26

Table 9.4: Two methods for calculating the **erosion rate** of $CaCO_3$ by *E. mathaei* at Abu Ali based on: (a) **Method I**: the evacuation rate of dry gut contents and the average proportion of $CaCO_3$ in them (from Table 9.1; see Downing and El-Zahr (1987)); (b) **Method II**: the evacuation rate of $CaCO_3$ (see McClanahan and Kurtis, 1990). Population estimate is taken from Chapter 8.

(a)

Season	Total $CaCO_3$ over 24 hrs (g)	No. urchins (*n*)	Mean $CaCO_3$ content (g urchin^{-1} day^{-1})	Erosion Rate: $CaCO_3$ (g urchin^{-1} day^{-1})	Population size (m^{-2})	Erosion Rate: $CaCO_3$ (g m^{-2} day^{-1})
Summer	30.099	56	0.537	0.537	6.5	3.49
Winter	53.362	59	0.904	0.904		5.88

(b)

Season	Evacuation Rate: $CaCO_3$ / test size (g mm^{-1} urchin^{-1} hr^{-1})	Evacuation Rate: $CaCO_3$ / test size (g mm^{-1} urchin^{-1} day^{-1})	Mean Test size (mm)	Erosion Rate: $CaCO_3$ (g urchin^{-1} day^{-1})	Population size (m^{-2})	Erosion Rate: $CaCO_3$ (g m^{-2} day^{-1})
Summer	0.0004	0.0096	(51.05)	(0.490)	6.5	(3.19)
Mean			50.45	0.484		3.15
Winter	0.0004	0.0096	(49.89)	(0.479)		(3.11)

Table 9.5: Two methods for calculating the **erosion rate** of $CaCO_3$ by *E. mathaei* at Abu Ali based on; (a) **Method III**: the average $CaCO_3$ content in the gut over 24 hrs (see Bak, 1990). Population estimate is taken from Chapter 8; (b) **Method IV**: the evacuation rate of $CaCO_3$ as a proportion of test size (from Table 9.7).

	n	**Mean gut fullness (% WG / WB wt)**	**Mean $CaCO_3$ weight (g)**	**Mean % $CaCO_3$ in gut**
Before starvation	3	11.29 ± 1.30 (1.28, $n = 5$)	0.25 ± 0.13 (0.05)	29.29 ± 15.40 (6.20)
After starvation for 5 days	5	5.81 ± 1.34 (1.08)	0.19 ± 0.15 (0.12)	44.36 ± 18.02 (14.52)
After foraging on reef substrate for 5 days	6	10.20 ± 0.85 (0.81)	0.93 ± 0.37 (0.35)	43.98 ± 10.89 (10.38)
After foraging on settlement plates for 5 days	10	11.49 ± 1.14 (1.59)	0.95 ± 0.26 (0.36)	36.51 ± 1.14 (1.59)

Table 9.6: Mean gut fullness (% wet gut / wet body weight) and $CaCO_3$ content of the guts (x ± 95 % confidence limits, SD in parentheses) after **starvation** and subsequent **gut filling** in two different treatments (i.e., reef versus settlement plate).

	ANOVA (2-way with replication)			Mean ± 95% Confidence limits (SD in parentheses)		
	n	**Season**	**Time**	***n***	**Summer**	**Winter**
Diel feeding experiment	117	NS $p > 0.1$	NS $p > 0.5$	60	51.05 ± 1.12 (4.17, $n = 57$)	49.89 ± 1.45 (5.59)
Gut evacuation experiment	120	NS $p > 0.1$	NS $p > 0.1$	60	51.04 ± 1.26 (4.86)	50.19 ± 1.04 (4.01)

Table 9.7: **ANOVA** results of the diel feeding and gut evacuation experiments for **test size**. Means with 95 % confidence limits are also given. S = significant, NS = non-significant, SD = standard deviation. (The interaction term was non-significant in all cases).

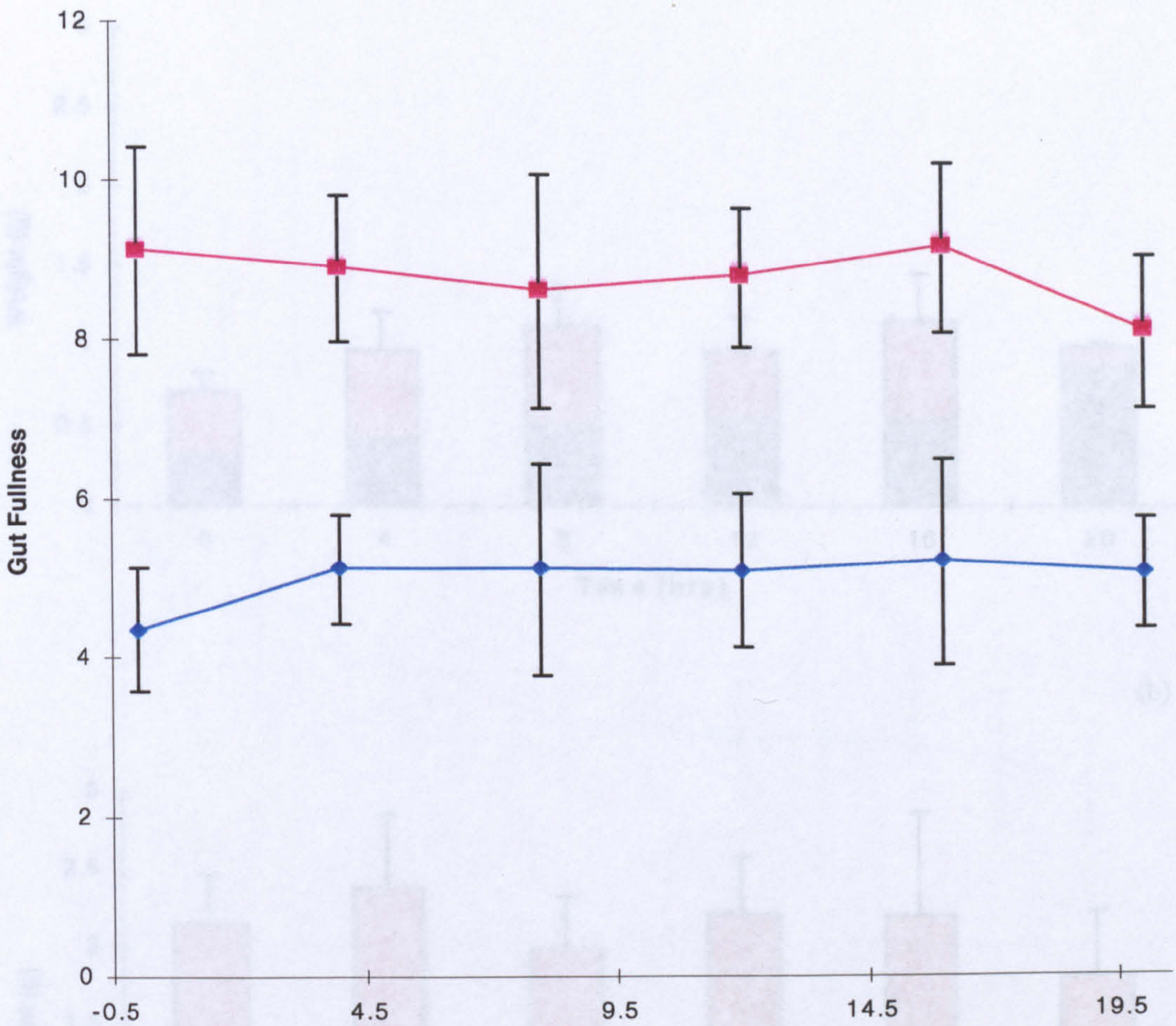


Figure 9.1: Average **gut fullness** (% wet gut weight/wet body weight; $x \pm SD$, $n = 10$) over a **24-hour period** (sunrise to sunrise) during summer (◆) and winter (■).

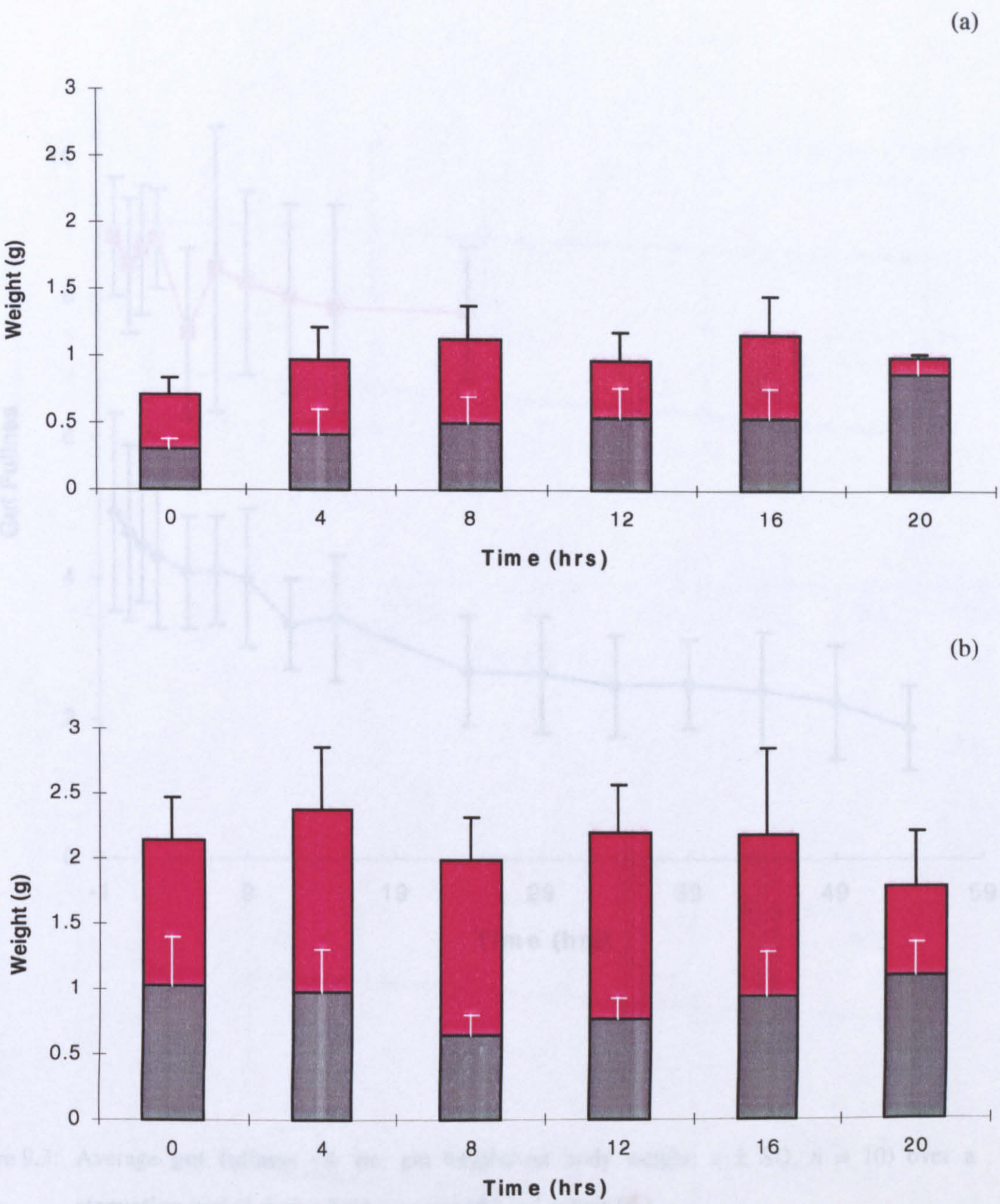


Figure 9.2: Relative fractions of **dried gut contents** ($x \pm SD$, $n = 10$) over a **24-hour period** (sunrise to sunrise); (a) summer (b) winter, and (■) $CaCO_3$ material (■) residual (mostly organic) material.

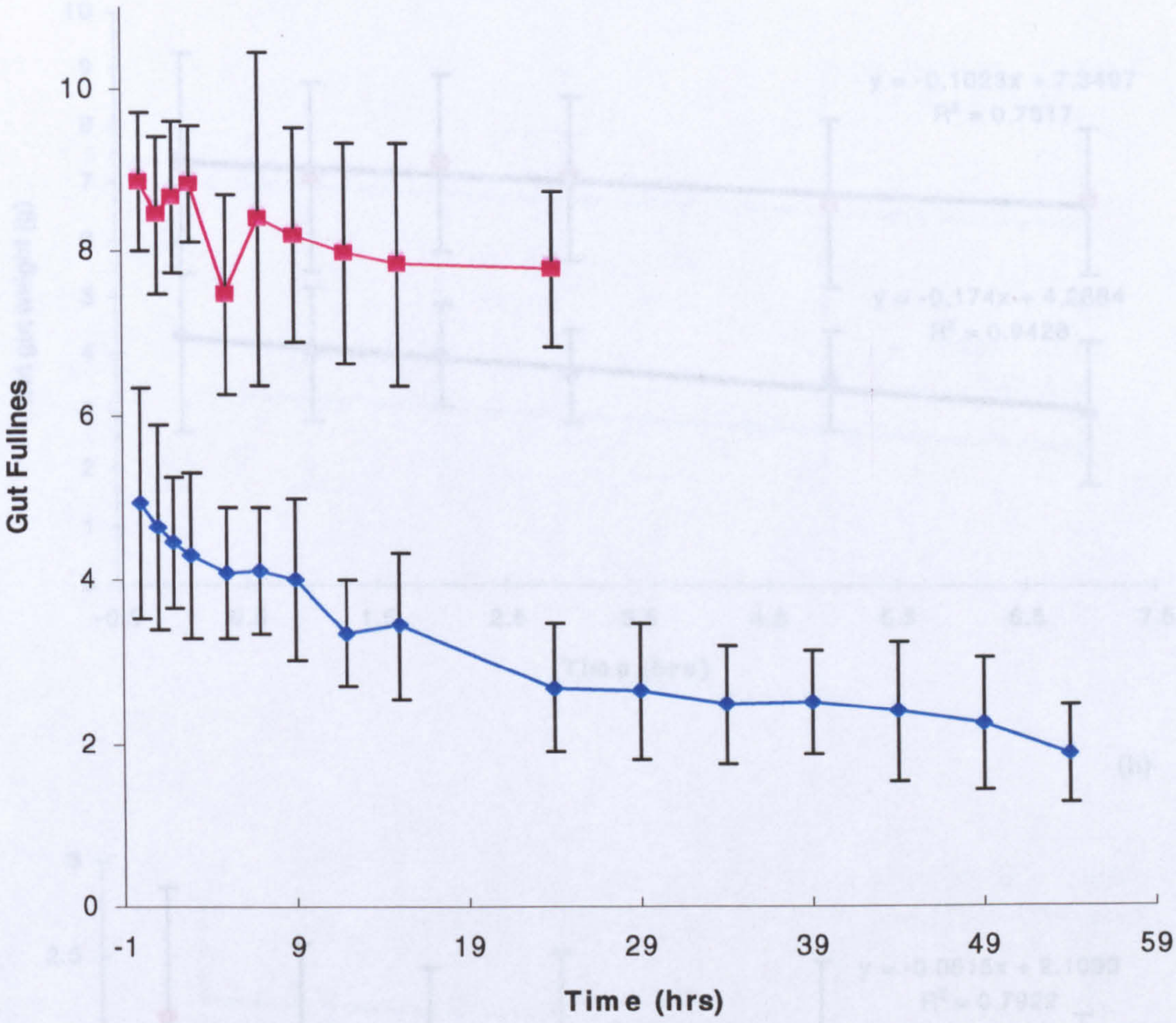
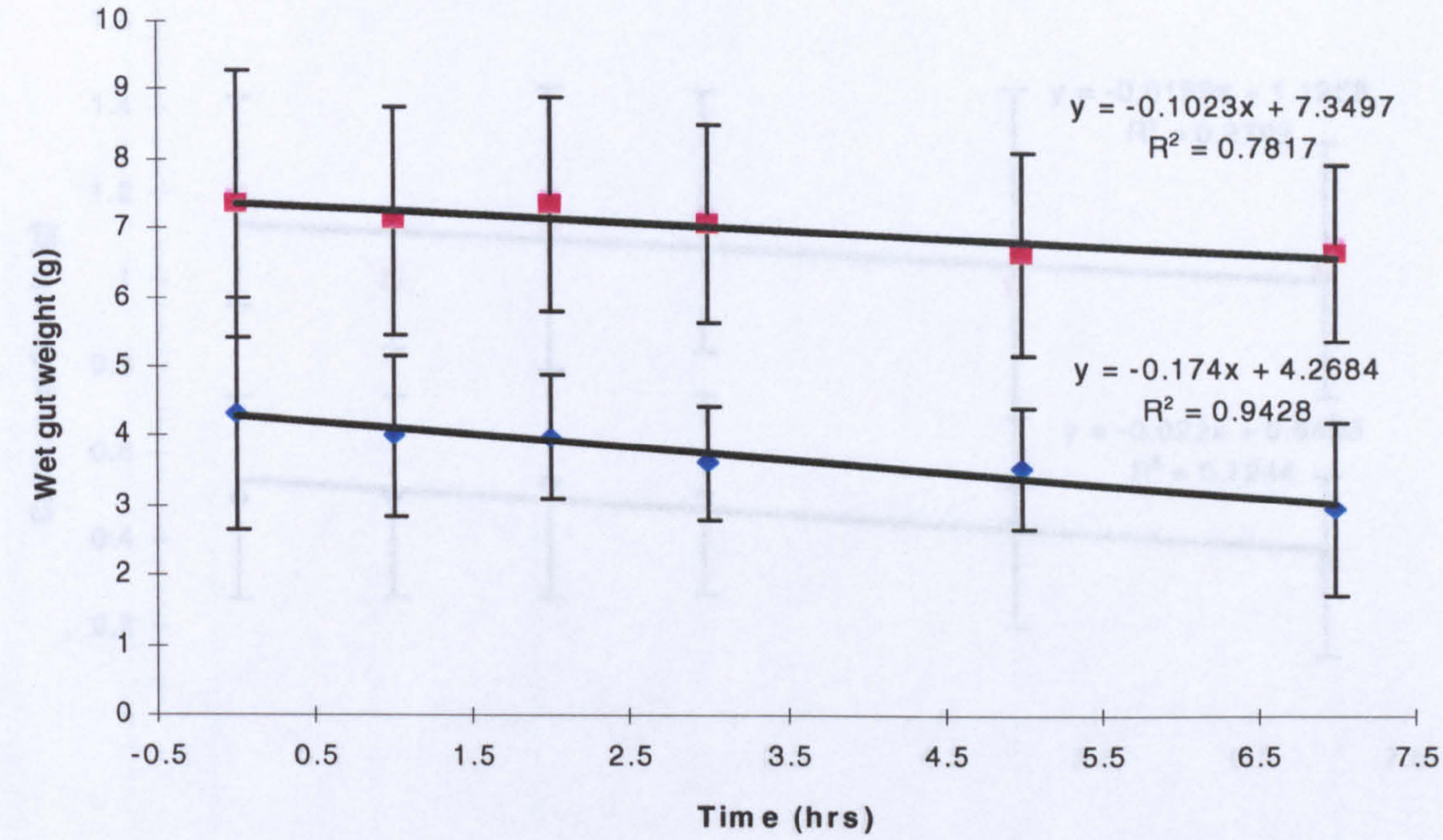


Figure 9.3: Average **gut fullness** (% wet gut weight/wet body weight; $x \pm SD$, $n = 10$) over a **starvation** period during both summer (◆) and winter (■).

(a)



(b)

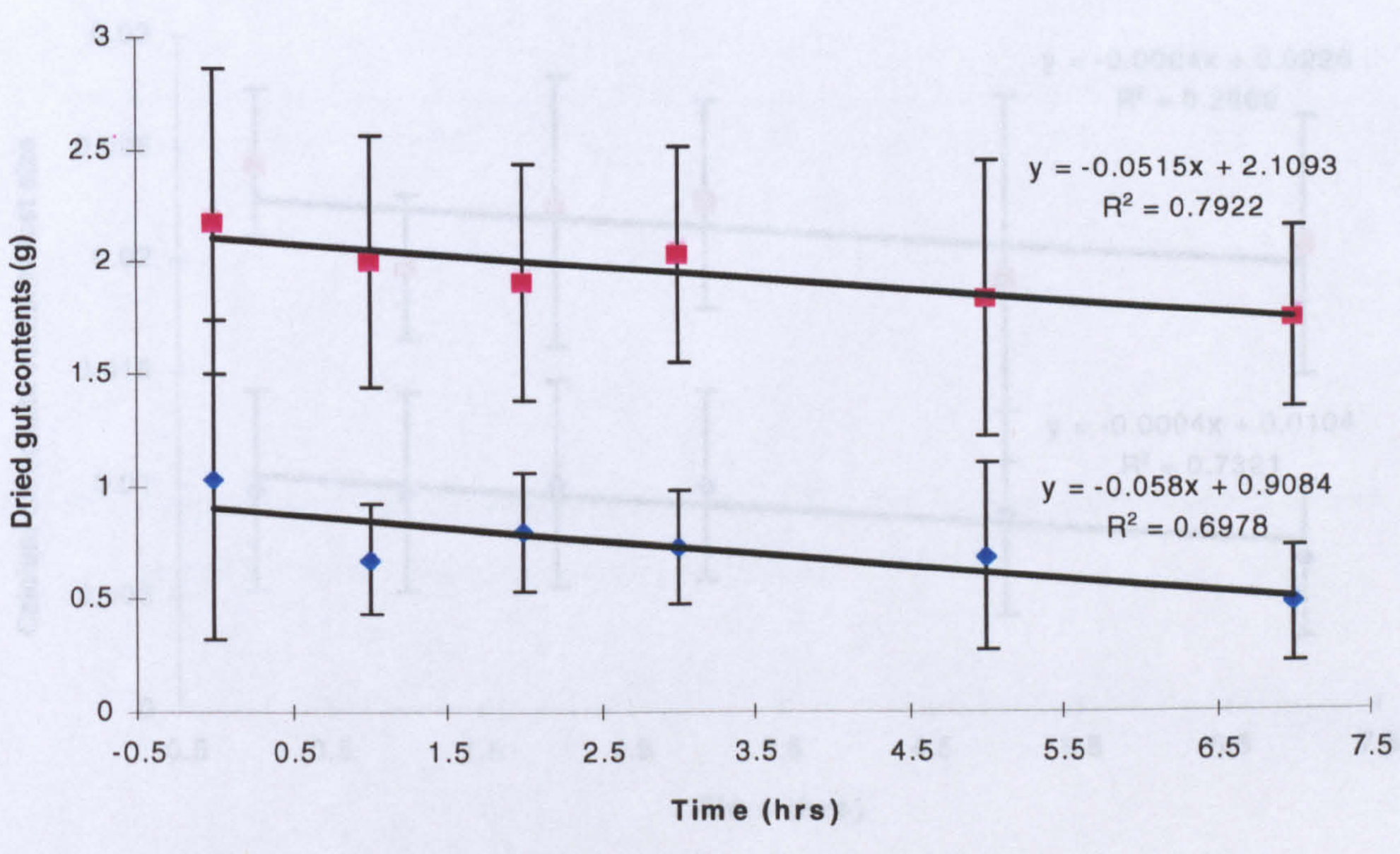


Figure 9.4: Total **gut evacuation** over **7-hrs** ($x \pm SD$; $n = 10$) during summer (◆) and winter(■); (a) **wet gut weight** (b) **dried gut contents**.

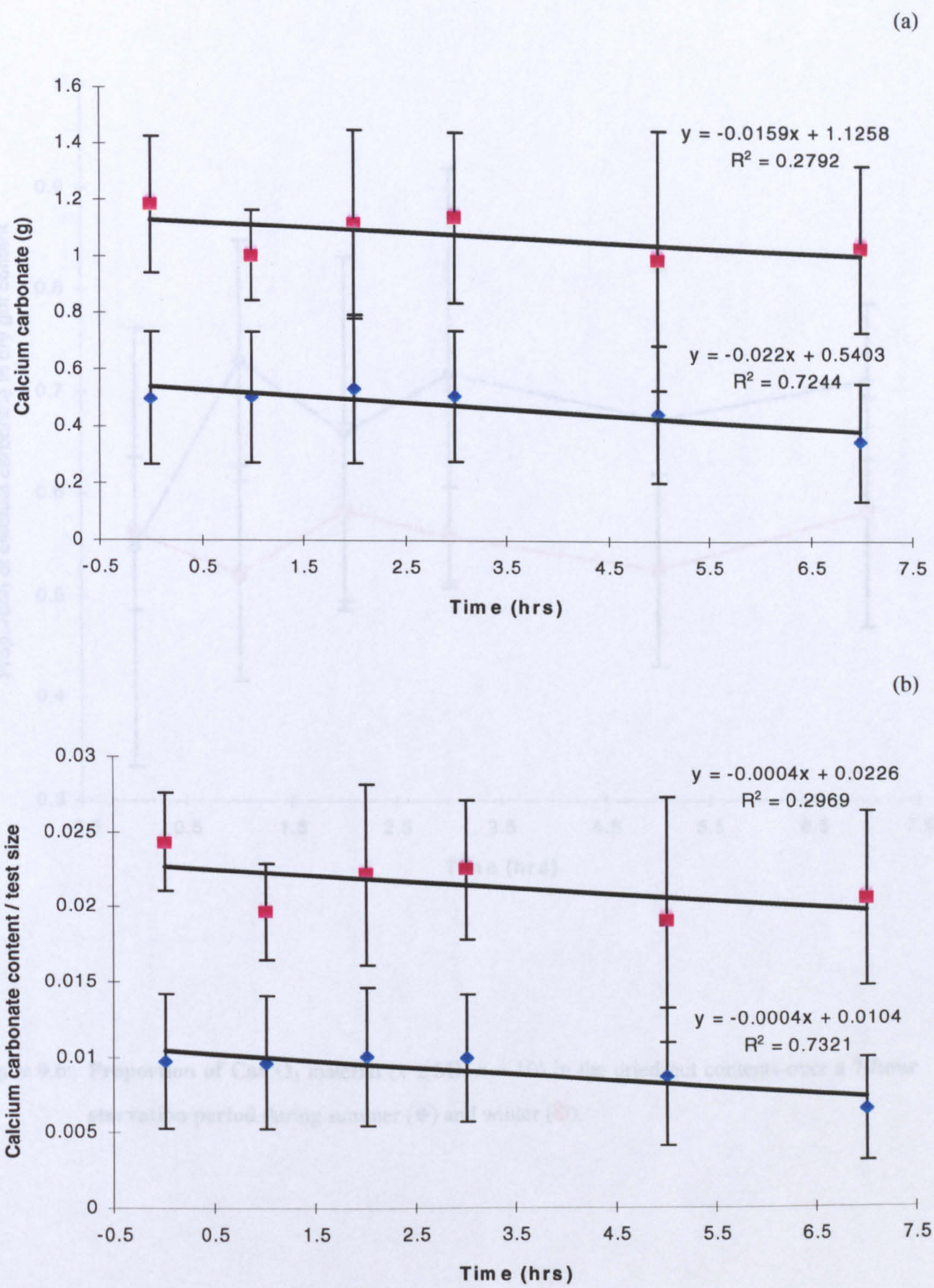


Figure 9.5: **Evacuation of $CaCO_3$** material (dry weight; $x \pm SD$, $n = 10$) over a **7-hour starvation period** during summer (◆) and winter (■); (a) **actual $CaCO_3$** weight (b) **ratio of $CaCO_3$** weight and test size.

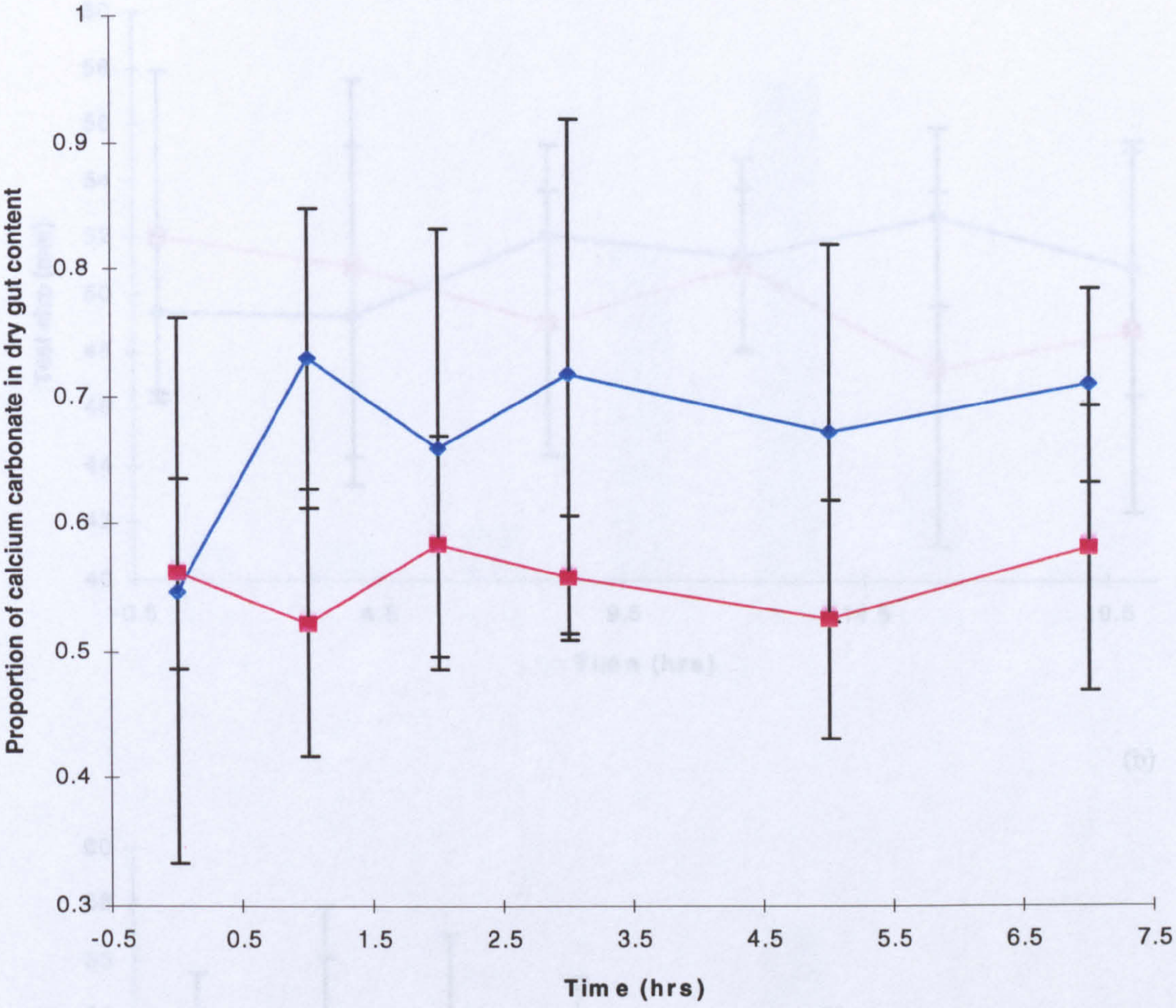
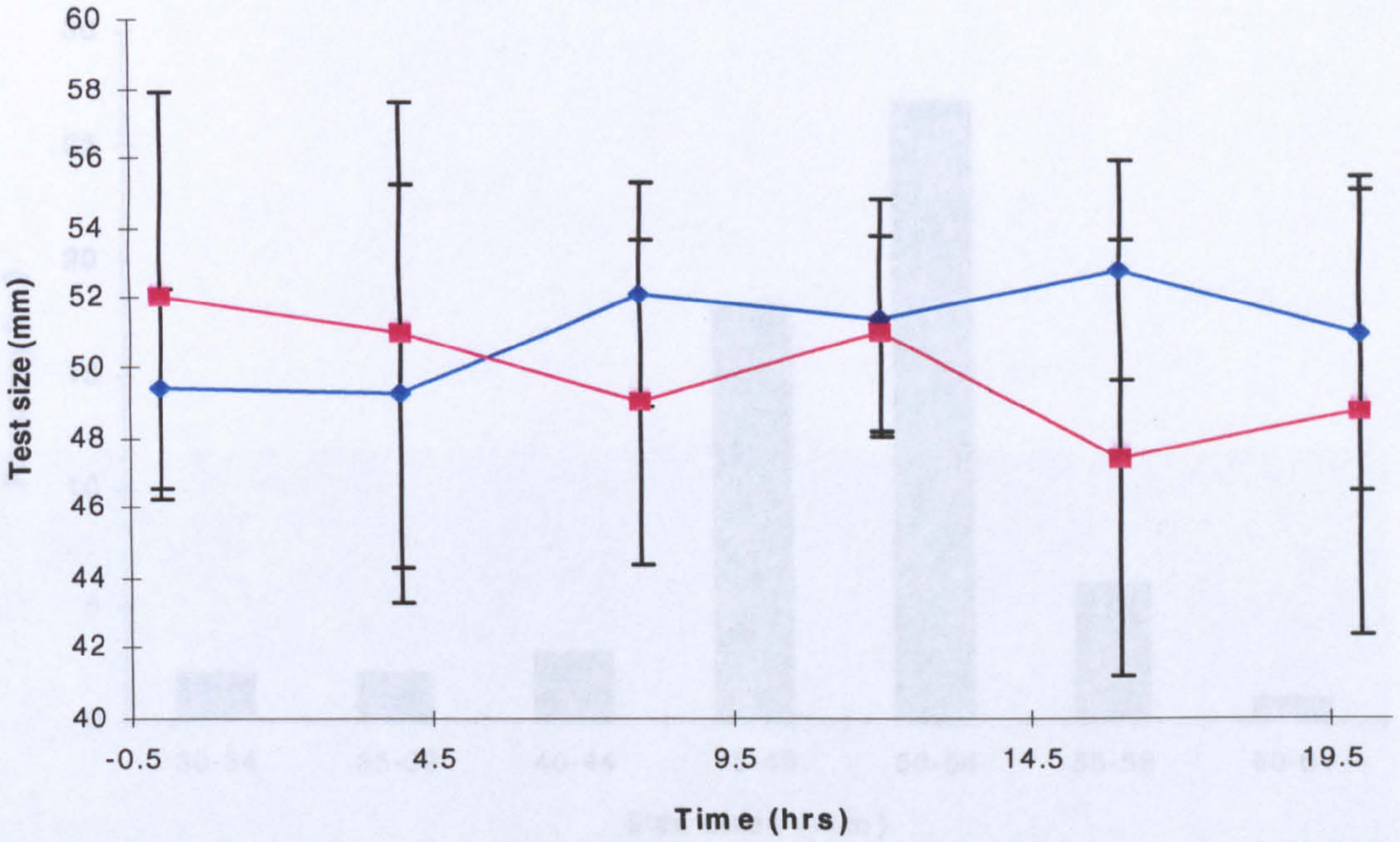


Figure 9.6: **Proportion of $CaCO_3$** material ($x \pm$ SD, $n = 10$) in the dried gut contents over a **7-hour starvation period** during summer (◆) and winter (■).

(a)



(b)

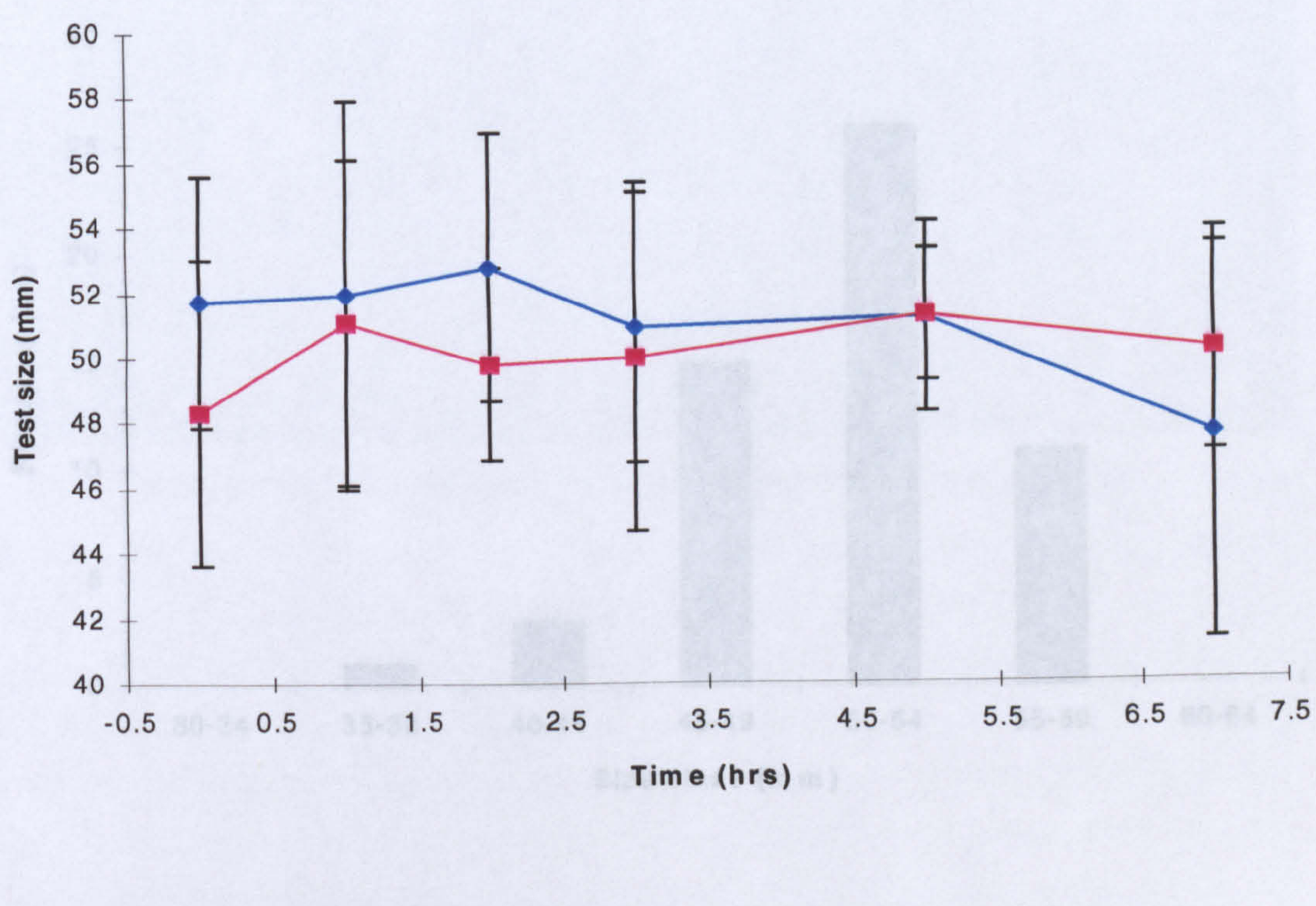


Figure 9.7: Average **test size** [(long axis + short axis)/2] of the sampled urchins ($x \pm$ SD, $n = 10$) during the summer (◆) and winter (■); (a) **diel experiment** (b) **evacuation experiment**.

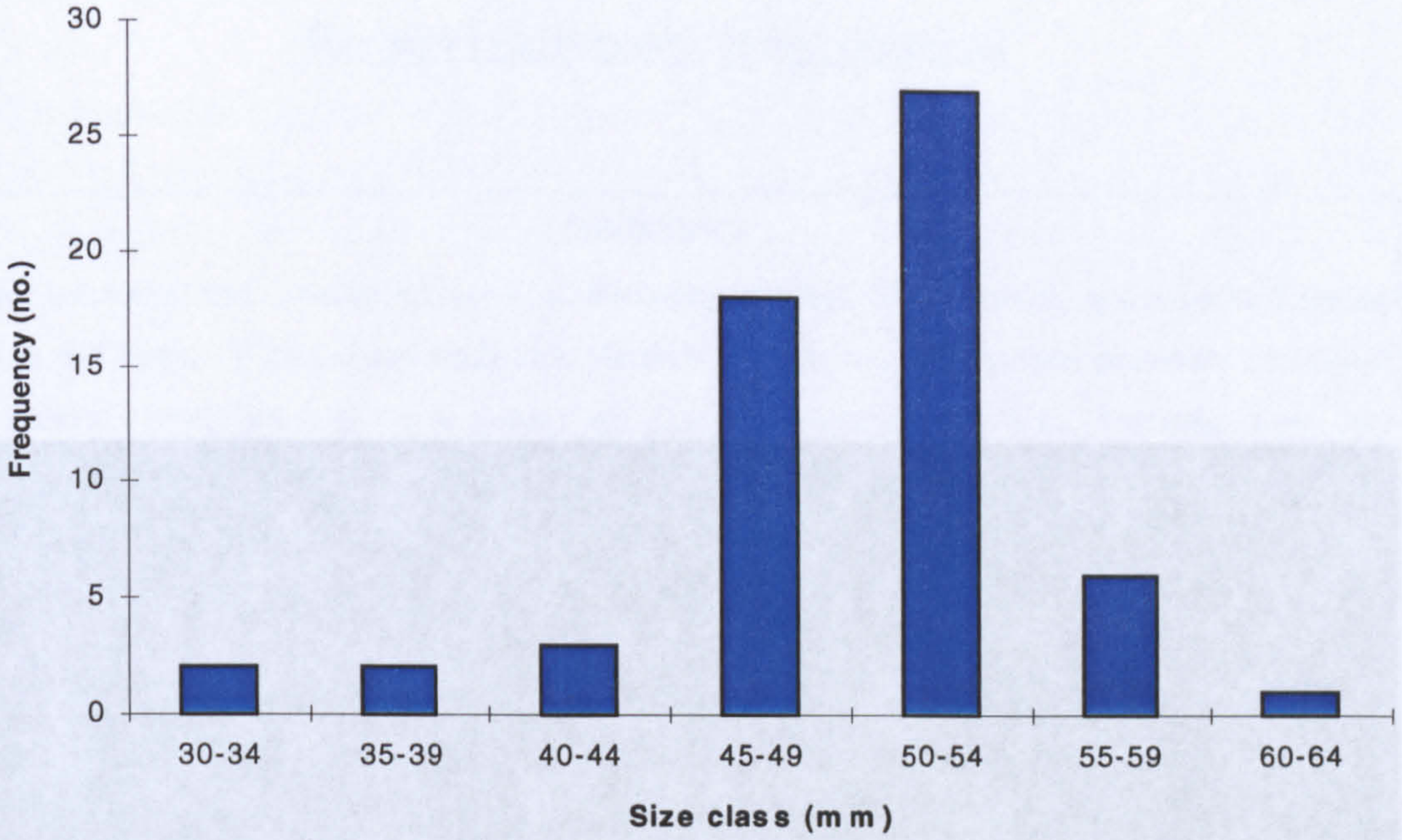


Figure 9.8: **Frequency of test size** [(long axis + short axis)/2] classes for those urchins sampled during the diel experiment; (a) summer (b) winter.

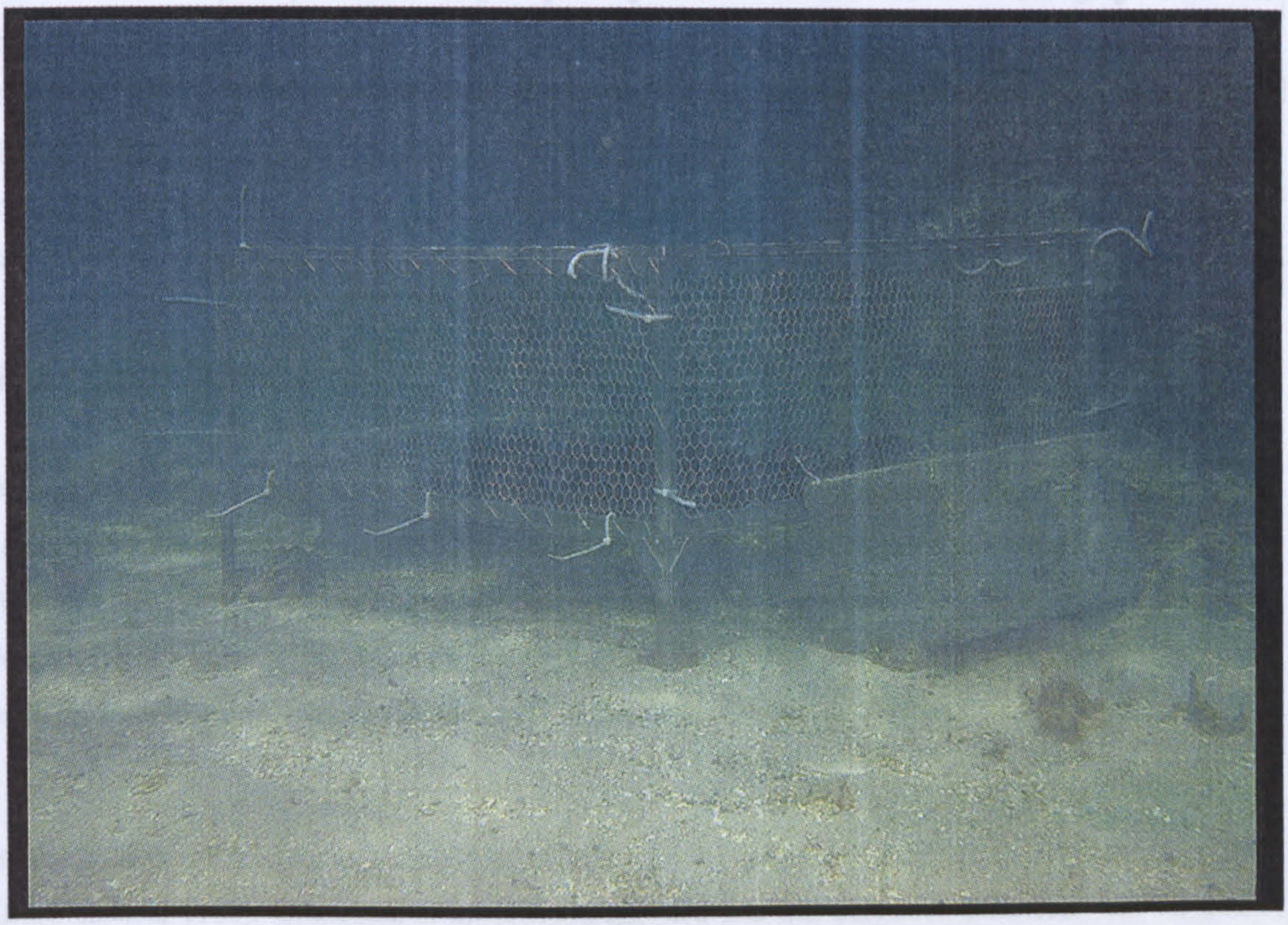


Plate 9.1: Starvation cage for *E. mathaei* at the inshore fringing reef at Abu Ali (17/8/94).

Chapter Ten

Behaviour and Regulation

Summary

Burrow behaviour and foraging activity of *Echinometra mathaei* (de Blainville) was examined during summer and winter at the inshore study site. Burrow defence and fidelity were positively correlated with burrow complexity, and the frequency of agonistic behaviour was low. Foraging range was negatively correlated with burrow complexity and the average distance covered was larger in summer than in winter, probably due to seasonal differences in environmental conditions and food abundance. Since neither predators nor predation events were recorded within a 24-hour period and the frequency of agonistic behaviour was low, it was concluded that the risk of adult mortality from predation was small.

10.1 Introduction

Agonistic behaviour has been shown to exist in a variety of echinoid species, both inter- and intraspecifically (McClanahan, 1988; Shulman, 1990). This aggressive behaviour manifests itself in the form of either *pushing* with spines and test or the *biting* of spines and test (Grünbaum *et al.*, 1978). The former appears to be primarily employed by sturdy, short-spined varieties (i.e., *Echinometra*) and the latter by more delicate, long-spined genera (i.e., *Diadema*) (Shulman, 1990).

Such aggressive behaviour is normally associated with the defence of an excavated burrow or crevice (McClanahan, 1988). Grünbaum *et al.* (1978) suggested that this defensive behaviour was for either food resources or the protection afforded by the burrow itself. However, McClanahan and Kurtis (1991) discovered that the population density of *E. mathaei* was inversely related to aggressive behaviour, and therefore burrow defence was predominantly correlated to predation risk, and not food limitation. Yet in addition to predation, the burrows shelter individuals from potentially damaging environmental effects, such as wave exposure. For example, *E. mathaei* is commonly associated with exposed, reef crest habitats (Khamala, 1971; Russo, 1980), where burrows and crevices aid the urchins' anchoring in such high energy areas. Burrowing behaviour in such habitats has also been associated with sedentary feeding behaviour whereby the urchins gain sufficient resources from algal detritus and other drift-food washed into the burrows (Hart and Chia, 1990). However, limiting food resources have been shown to trigger exposed foraging behaviour (Hart and Chia, 1990) unless limited by predation pressure (Carpenter, 1984). For example, Levitan and Genovese (1989) have shown that urchins respond to predation pressure by restricting their distribution to reef habitats with suitable refuges.

Hence there is a trade-off between the risk of mortality from predation and the energetic costs of remaining in high density, food limited conditions.

The aims of the following study were three-fold. Firstly, to estimate the average foraging distance travelled by *E. mathaei* during daylight hours in summer and winter and thereby investigate the relationship between environmental conditions and foraging activity. Secondly, to investigate the level of agonistic behaviour between individuals exhibiting similar burrowing strategies, and finally to estimate the risk of mortality due to fish predation events.

10.2 Materials and Methods

10.2.1 Agonistic behaviour

Observations of urchin behaviour at the inshore study site identified three strategies of burrow fidelity:

Closed -	inhabiting an enclosed burrow
Open -	inhabiting an open burrow/ depression
None -	no burrow, ranging over open substrate

Five urchins expressing each type of burrow behaviour were randomly selected. At time zero an urchin of equivalent size was placed in direct contact (spines touching) with the subject urchin. The behaviour of the two urchins was then observed for a maximum of 20 minutes and the outcome of the interaction recorded. The results were recorded under the following categories:

no fight -	urchins remain in contact - coexistence
no fight -	urchins break contact
fight -	intruder leaves
fight -	host leaves

This experiment was conducted in summer (August 1994) and winter (January 1995).

10.2.2 Diurnal foraging behaviour

Three groups of six urchins were randomly selected and tagged by placing labelled, plastic cable-ties over their spines. Using an underwater compass weighted to the substrate, the bearing and distance of each urchin from this static point was measured every hour throughout the diurnal period (Plate 10.1). The foraging trail and total distance travelled was then extrapolated (i.e. triangulation/trigonometric theory). Two of the urchin groups monitored were exhibiting the same burrow strategy, *none*, while the

third group exhibited *open* burrowing. This experiment was conducted in summer (August 1994) and winter (January 1995).

10.2.3 Predation pressure

Predation pressure on *E. mathaei* at Abu Ali was estimated using a tethering technique developed by McClanahan and Muthiga (1989). At dawn, prior to the feeding trial, ten urchins were randomly selected from the reef and, using Vernier callipers, their individual diameters were measured (to 0.1 mm). Each urchin was then tethered to a monofilament line. The procedure involved the urchin test being pierced by a hypodermic needle and threaded with a 0.5 mm diameter line. The tethered urchins were then fixed at 1 m intervals along a 10 m line that was weighted at both ends and stretched out across the reef, parallel to the shore.

The line was monitored for one hour during which period the following observations were recorded:

(i) The time taken for each urchin to be successfully attacked.
(ii) The species of predator which attacked each urchin.
(iii) The time taken for each predator to consume each urchin.

The feeding trials were performed in summer (August 1994) and winter (January 1995).

10.3 Results

10.3.1 Agonistic behaviour

All urchins expressed similar levels of antagonism towards conspecifics during summer and winter (Table 10.1). Those exhibiting *closed* burrow behaviour were more pre-disposed to aggression with the intruder being forced to leave in all cases. In contrast, those urchins exhibiting *no* burrowing behaviour showed no aggressive responses, while *open*-burrow individuals held the intermediate position showing an almost equal disposition for either aggression or coexistence. Furthermore, of those that did fight, the majority resulted in coexistence (CE) while the remainder were recorded as intruder leaving (IL). The time taken to complete all of these responses (to maximum of 20 mins) did not vary significantly between burrow type or season (ANOVA (2-way with replication), $n = 30$, $p > 0.05$ in both cases).

10.3.2 Diurnal foraging behaviour

Over the entire diurnal period, urchins exhibiting *no* burrowing behaviour in summer moved, on average, approximately five times further and faster than similar-sized individuals exhibiting *open* burrowing behaviour. For urchins in the winter study, the difference was only two-fold (Table 10.2).

In addition, *no* burrowing behaviour was also three times faster during summer than winter, while the rate of movement observed for *open* burrowing behaviour was similar between seasons. It is important to note that the total distances travelled are not directly comparable between the seasons due to a difference in diurnal length; thirteen hours in the summer compared to only nine hours in the winter.

Examination of the distance moved each hour revealed different levels of activity throughout the diurnal period, for both burrowing behaviour and season (Figures 10.1 and 10.2). In summer, foraging activity was greatest during the latter half of the diurnal period (i.e., from midday to late afternoon). In contrast, the winter activity pattern was greatest at the beginning and end of the diurnal period (i.e., sunrise and sunset). The existence of different seasonal behavioural activity is only tentatively suggested, due to the high level of variability in distances travelled by different individuals (see error bars in Figure 10.1).

The foraging patterns displayed by *exposed* individuals in summer were variable and wide-ranging (Figures 10.3 and 10.4). They also formed aggregations at the beginning and end of the diurnal period. Those individuals in *open* burrows remained either inside or in close proximity to their burrows (Figure 10.4). In winter, all urchins displayed comparatively similar patterns and ranges (Figures 10.5 and 10.6).

10.3.3 Predation

No predation events were recorded during the first hour or the subsequent 24-hour period, in either summer or winter.

10.4 Discussion

Echinoid burrow excavation and defence has been shown to be positively correlated with availability of drift food (Hart and Chia (1990), wave exposure (Grünbaum *et al.*, 1978) and predation risk (McClanahan and Kurtis, 1991). At Abu Ali the *none* and *open* burrowing behaviours were the dominant forms, while *closed* burrows occurred very rarely (pers. obs.). This preference for increased exposure implied either low predation risk, food-limiting conditions and/or insufficient risk of dislodgement and damage due to wave exposure. The reduced risks of mortality from predation or starvation were most probably due to the absence of any fish predators recorded in the area and the abundance of benthic algae (Chapter 5).

The frequency of agonistic behaviour was correlated with burrow complexity, and given the observed scarcity of *closed* burrows, burrow defence was therefore not prevalent amongst the *E. mathaei* population at Abu Ali. This gives further support to the conclusion that the urchins were not exposed to high adult predation mortality since the frequency of burrow defence and fidelity has also been

correlated with predation risk (Carpenter, 1984; Levitan and Genovese, 1989; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991).

The rare occurrence of burrowing behaviour without any clear reasons for it (though possibly wave exposure) may have been an instinctive response. Indeed, predisposition towards aggression and burrow excavation has been argued as evidence for a distinction between sub-species, (i.e. *E. mathaei oblonga* and *E. mathaei mathaei*). Neill (1988) (Guam) and Tsuchiya and Nishihira (1985) (Japan), have demonstrated that transplanted individuals from an aggressive, reef edge population to a non-aggressive back-reef population, and vice versa, retained their former behavioural tendencies. However, McClanahan and Kurtis (1991) concluded from their studies on *E. mathaei* in Kenya that such contrasting behaviours were habitat-dependent and found no clear evidence for the presence of distinctive sub-species.

Burrow complexity was also correlated with reduced foraging distance and therefore individuals within burrows were more predisposed towards a sedentary life style and not merely using the burrow as a static point from which to forage. Homing behaviour and crevice fidelity has been observed during nocturnal foraging by *D. antillarum* (Carpenter, 1984). In the present study, however, nocturnal observations of foraging behaviour were not made and it is not clear whether the recorded diurnal relationships between burrow complexity and foraging ranges remained constant throughout the diel period.

Foraging ranges in winter were significantly smaller than those in summer. This was probably due to either environmental conditions (i.e. lower temperatures and increased wave action during winter; Chapter 4) and/or increased food abundance (i.e. benthic algal biomass; Chapter 5). If temperature alone was responsible for reducing behavioural activity, such as foraging, a similar decline in other behavioural responses might be expected. However, there was no significant seasonal difference in the frequency or duration of agonistic responses. Hence seasonal changes in food abundance was probably the principal factor (i.e. increased algal cover means less foraging is needed to acquire daily food requirements). The seasonal differences in foraging activity throughout the diurnal period may also be in response to environmental conditions. For example, the main seasonal difference in tidal patterns is that summer tides are comparatively higher, with the highest occurring during the diurnal period while the reverse situation occurs in winter (Chapter 4). A tentative conclusion, therefore, would be that urchin activity is correlated with maximum water depth over the reef when the effects of wave action are likely to be less severe. Furthermore, the summer diurnal activity pattern (i.e. maximum movement during the middle of the day) is consistent with the observed aggregations (i.e. periods of reduced activity) at sunrise and sunset. Aggregations in echinoid populations have been shown to form in response to spawning behaviour (Levitan, 1988a), and risk of predation (Pearse and Arch, 1969). In the present study, the former may have been more probable. Indeed, a spawning event was observed on 14 August 1994, a few days before the summer behavioural experiments were conducted.

In summary, the adult *E. mathaei* population at Abu Ali was not limited by predation and exhibited predominantly exposed foraging behaviour, which differed in terms of distance covered and diurnal activity between summer and winter.

(a)

Burrow behaviour:	***closed*** ($n = 5$)	***open*** ($n = 5$)	***none*** ($n = 5$)
Response	**Frequency (%)**	**Frequency (%)**	**Frequency (%)**
Fight:	**80**	**40**	**0**
HL	0	0	0
IL	100	0	0
CE	0	100	0
CB	0	0	0
No Fight:	**20**	**60**	**100**
HL	0	0	0
IL	100	0	0
CE	0	100	40
CB	0	0	60

(b)

Burrow behaviour:	***closed*** ($n = 5$)	***open*** ($n = 5$)	***none*** ($n = 5$)
Response	**Frequency (%)**	**Frequency (%)**	**Frequency (%)**
Fight:	**80**	**40**	**0**
HL	0	0	0
IL	100	50	0
CE	0	50	0
CB	0	0	0
No Fight:	**20**	**60**	**100**
HL	0	0	0
IL	100	0	0
CE	0	33	80
CB	0	67	20

Table 10.1: **Frequency of antagonistic response**, where; (a) summer (b) winter at Abu Ali. HL = host leaves; IL = intruder leaves; CE = coexistence; CB = contact broken.

Burrow behaviour:	Summer		Winter	
	None	*Open*	*None*	*Open*
Mean distance travelled in diurnal period (cm)	(n = 12) 283.06 ± 141.89 (223.41)	(n = 6) 56.75 ± 28.45 (27.05)	(n = 12) 71.24 ± 32.20 (50.68)	(n = 6) 33.16 ± 22.05 (21.01)
Mean distance travelled per hour (cm)	(n = 13) 21.77 ± 6.26 (10.36)	(n = 13) 4.37 ± 1.47 (2.44)	(n = 9) 7.92 ± 2.00 (2.60)	(n = 9) 3.69 ± 2.59 (3.37)

Table 10.2: Mean **diurnal foraging distances** and **movement rates** (x ± 95 % confidence limits, SD in parentheses) for *E. mathaei* at Abu Ali during summer and winter.

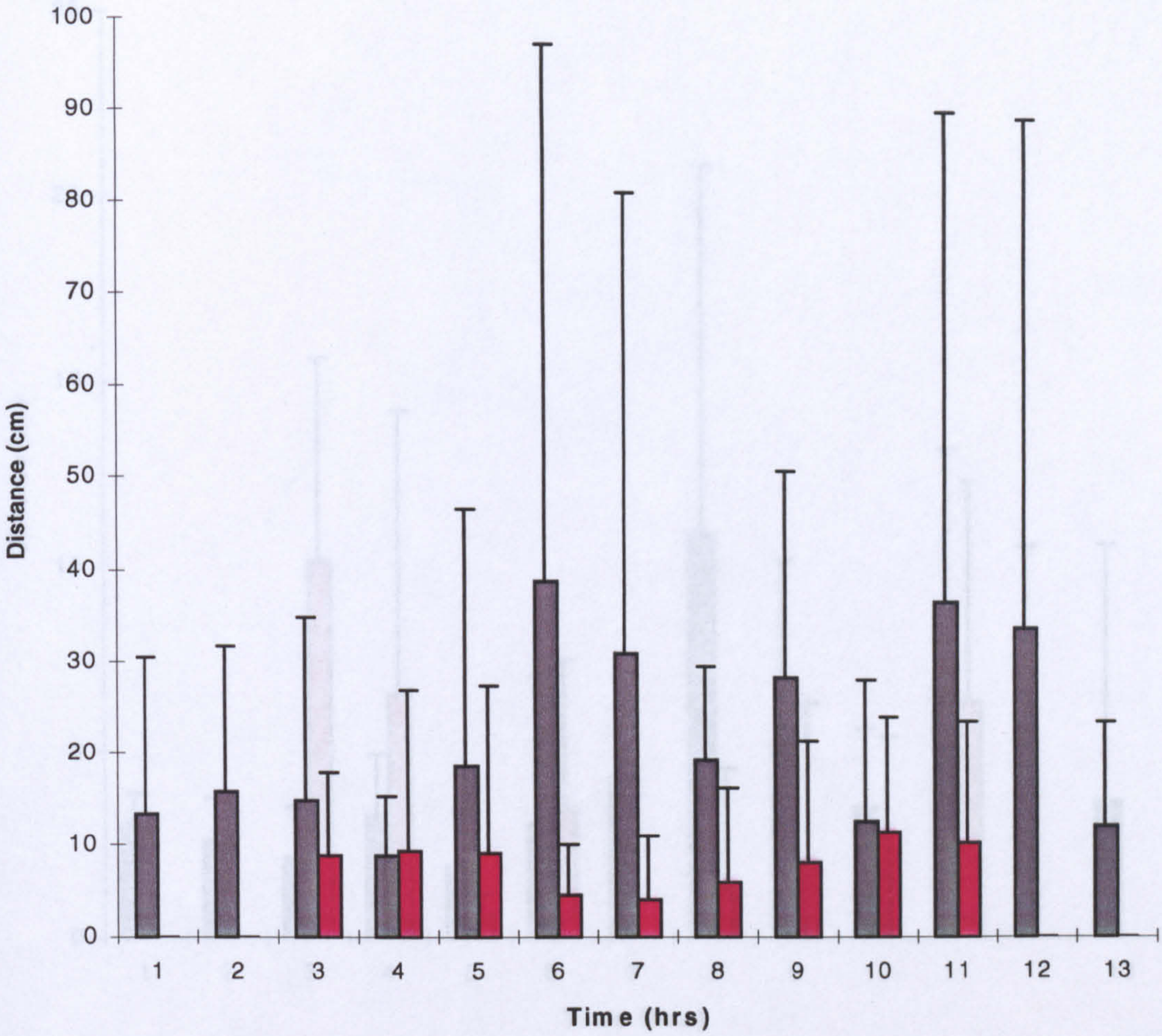


Figure 10.1: Average **distance travelled** per hour ($x \pm SD$, $n = 6$), throughout the **diurnal period** during summer (■) and winter (■) for those exhibiting ***no*** burrowing behaviour.

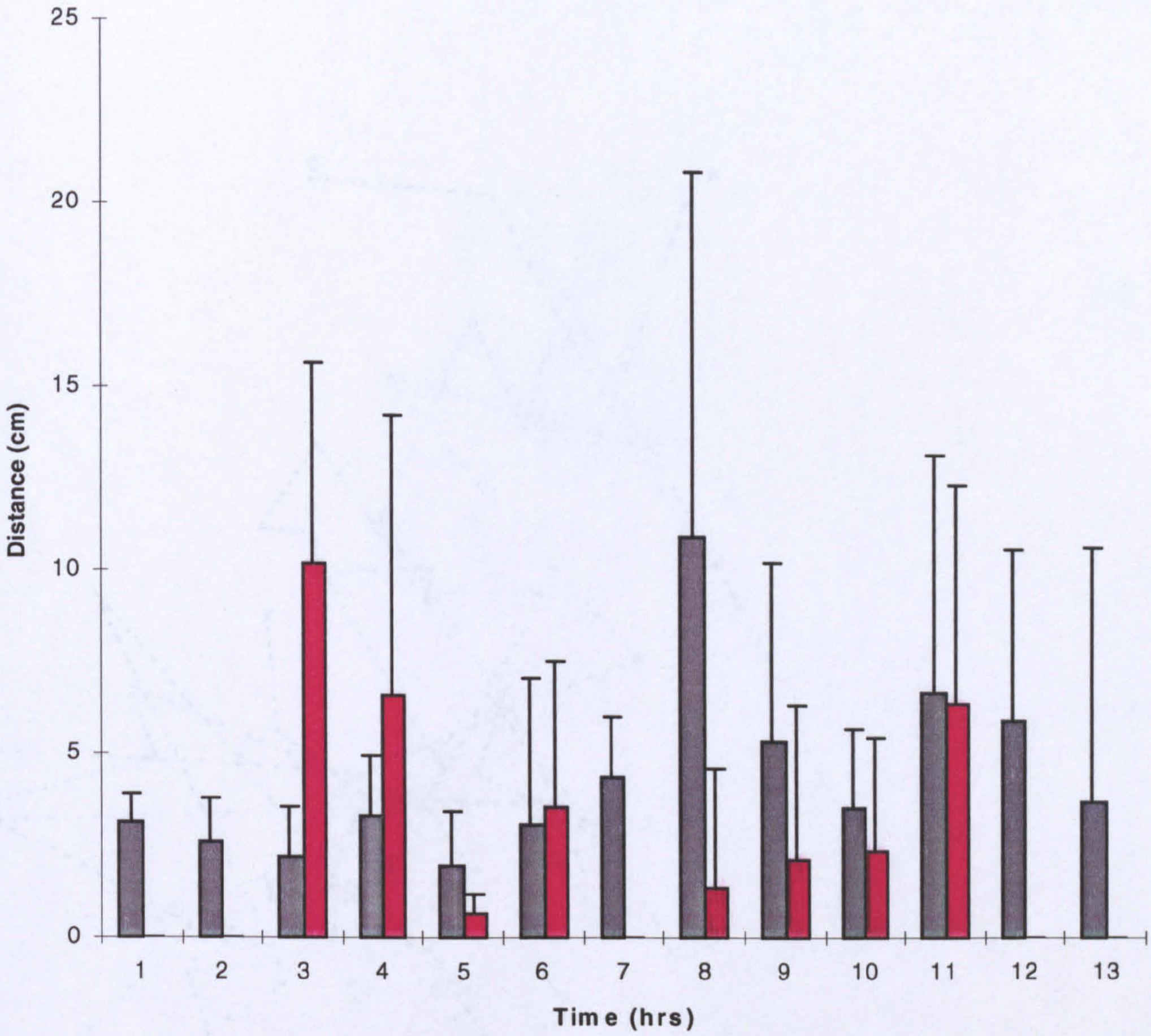


Figure 10.2: Average **distance travelled** per hour ($x \pm$ SD, $n = 6$), throughout the **diurnal period** during summer (■) and winter (■) for those exhibiting ***open*** burrowing behaviour.

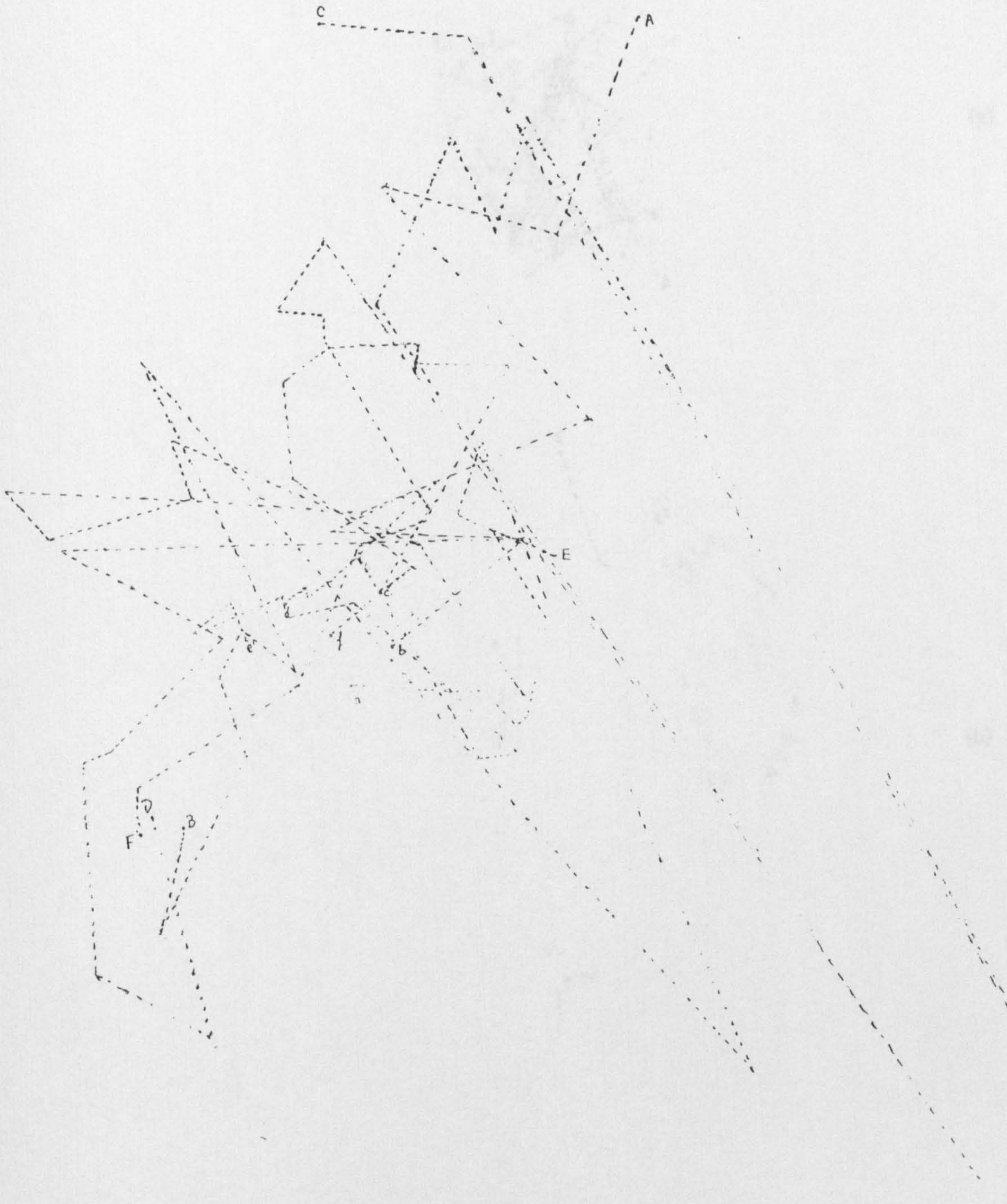


Figure 10.3: **Foraging patterns** of six urchins exhibiting ***no*** burrowing behaviour at Abu Ali during **summer** (Scale 1 : 10).

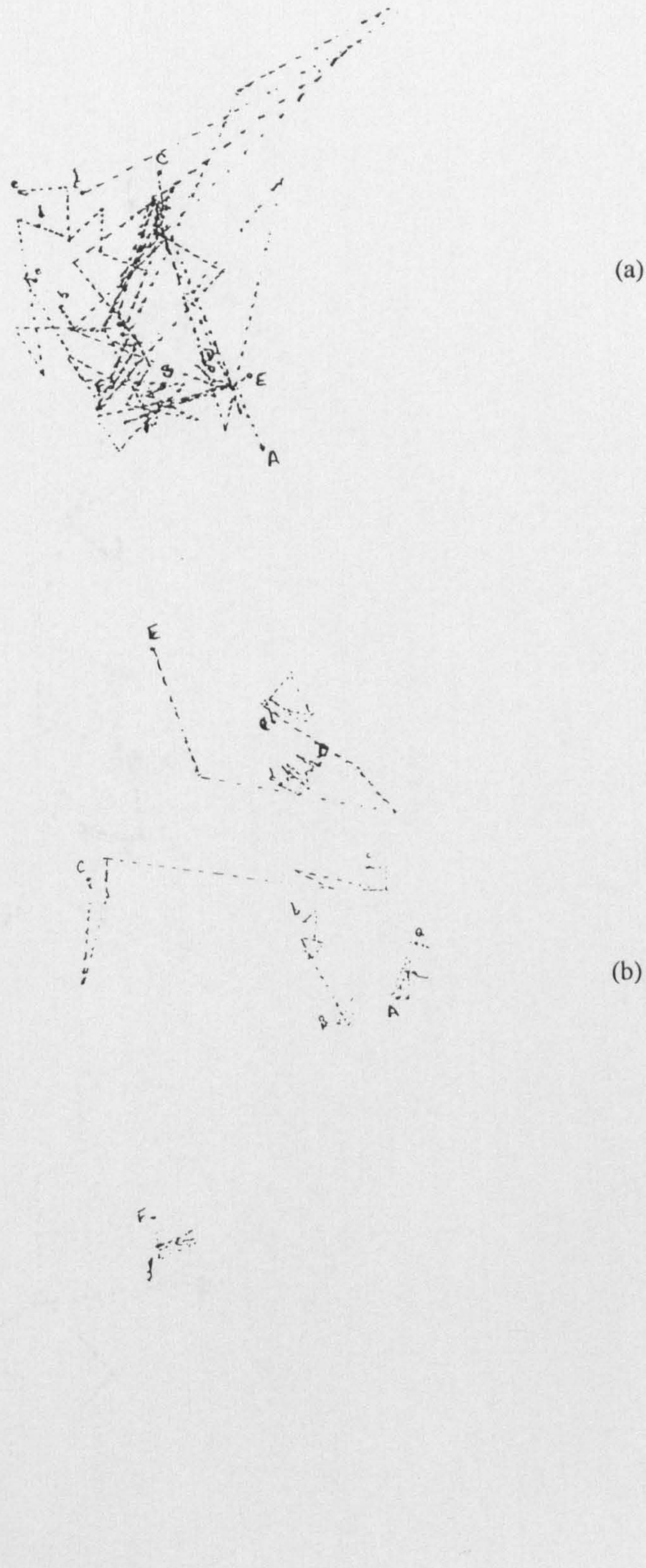


Figure 10.4: **Foraging patterns** of six urchins at Abu Ali during **summer** exhibiting (a) ***none*** (b) ***open*** burrowing behaviour (Scale 1 : 10).

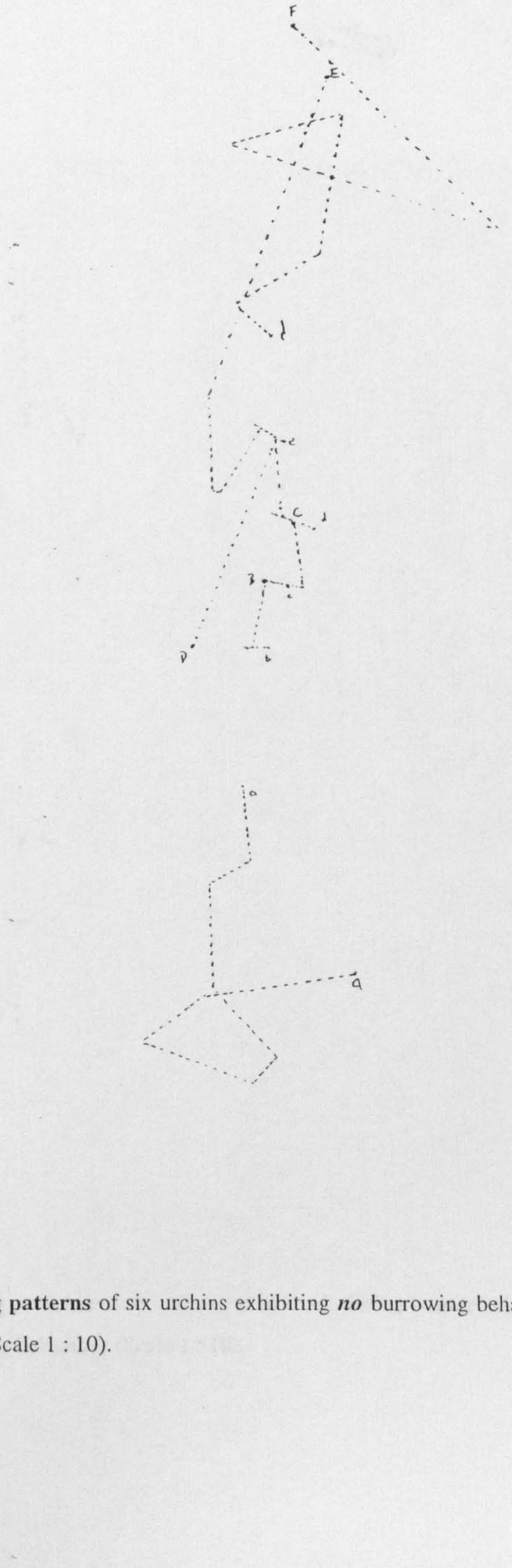


Figure 10.5: **Foraging patterns** of six urchins exhibiting ***no*** burrowing behaviour at Abu Ali during **winter** (Scale 1 : 10).

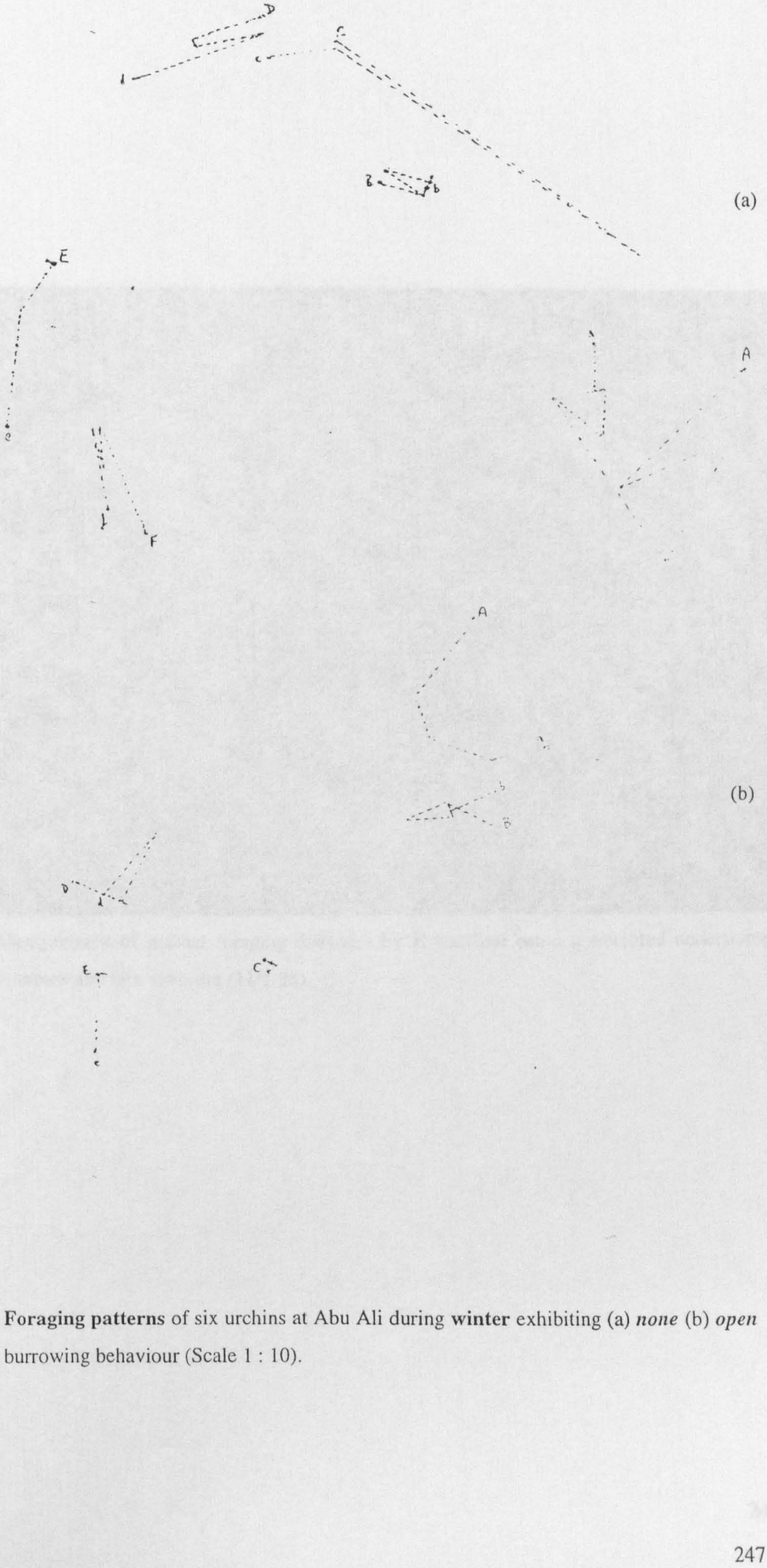


Figure 10.6: **Foraging patterns** of six urchins at Abu Ali during **winter** exhibiting (a) *none* (b) *open* burrowing behaviour (Scale 1 : 10).

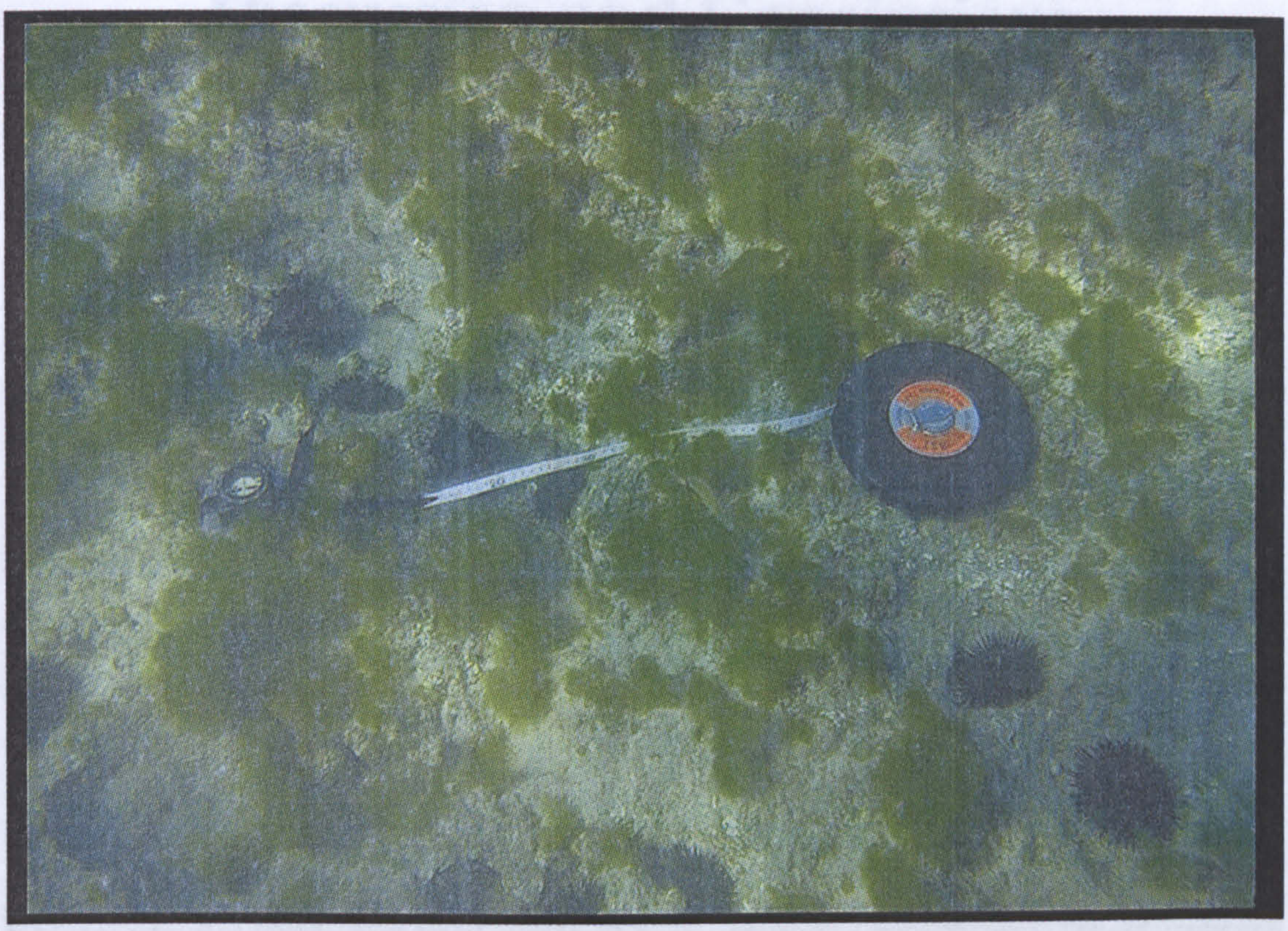


Plate 10.1: Measurement of diurnal foraging distances by *E. mathaei* using a weighted underwater compass and tape measure (11/1/95).

SECTION SIX

Discussion and Conclusions

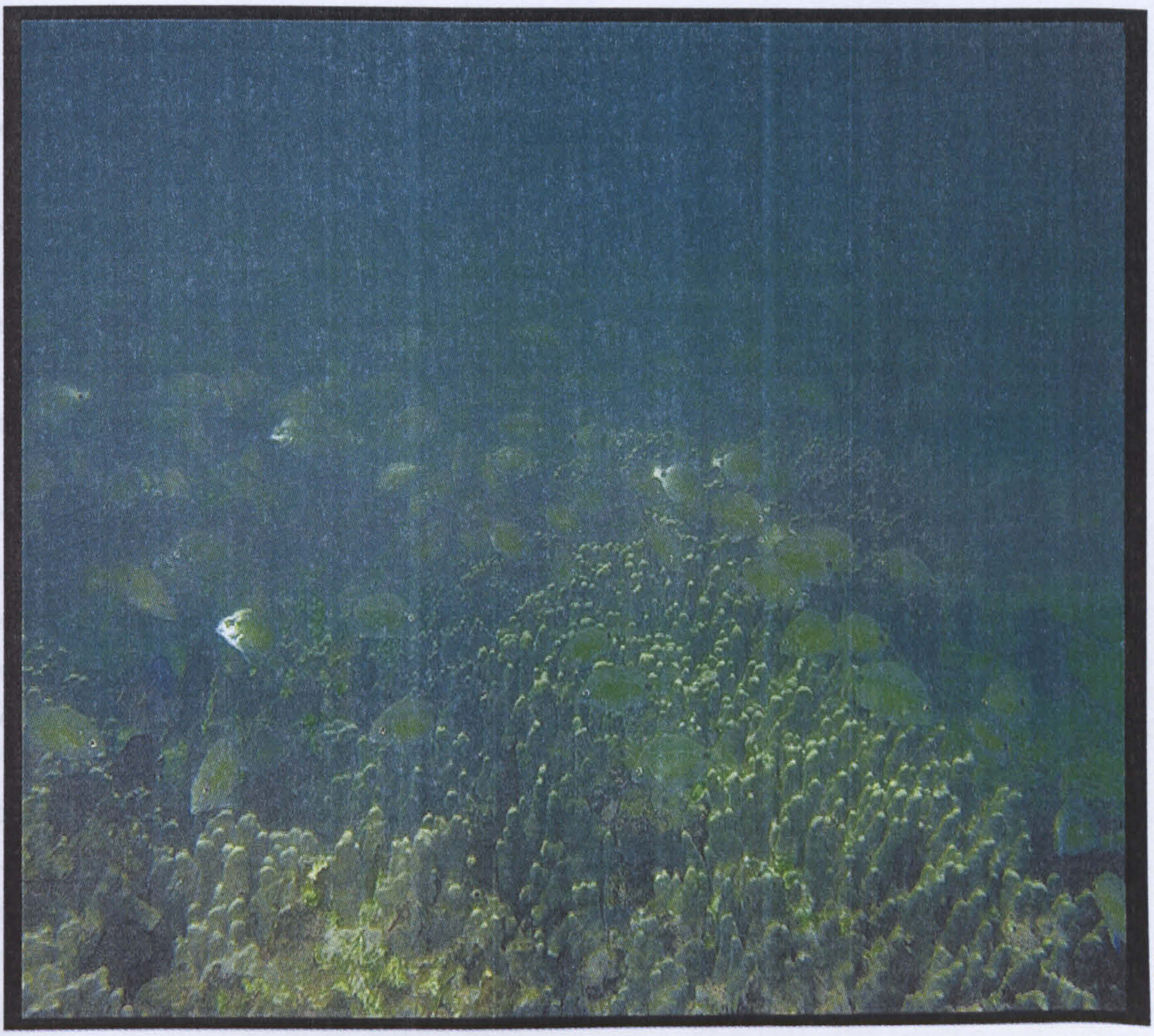


Plate 11.0: Shoals of *Diplodus sargus k.* congregated over the inshore fringing reef at Abu Ali (8/94).

Chapter Eleven

General Discussion and Conclusions

11.1 Experimental constraints and design

As with most ecological investigations, the main constraint to the fieldwork conducted in the present study was the weather. The Arabian Gulf experiences severe seasonal conditions (see Chapters 2 and 4), resulting in varying degrees of storm damage to the equipment deployed at the three study sites. This ranged from the loss of sediment trap replicates and minor vandalism of exclusion cages at the deep offshore site, to the loss of perturbation treatments and the entire exclusion experiment at the inshore study site after only two months.

In addition to damaged equipment, environmental conditions also imposed logistical constraints, particularly the number and duration of trips to the offshore study sites, which limited the extent of the fieldwork performed. For example, it prevented measurement of the bioerosive impact of the offshore echinoid populations for comparison with the inshore estimates.

A possible criticism of the experimental designs is the lack of study site replication, although each site was chosen as a representative of that particular reef habitat type. However logistical constraints, in terms of equipment and sampling time available, prevented the inclusion of replicate study sites. Logistical constraints also impaired the effectiveness and scope of some experiments. An example is the lack of nocturnal measurements of herbivore abundance and echinoid foraging behaviour.

Further constraints were also associated with the designs of the experimental equipment. For example use of artificial material for the algal settlement plates may have biased the composition of the colonising community. Their physical characteristics and orientation may have also enhanced sedimentation or influenced the behaviour of herbivores (see Chapter 5). However the overwhelming advantage of using artificial plates was their uniformity and availability for extensive deployment.

Despite the equipment damage and logistical constraints described, a large number of experiments were performed throughout an entire seasonal cycle. A wealth of new data was collected on many aspects of the herbivore community and its role within the coral reef ecosystems of the Saudi Arabian Gulf coast. The extensive time-series obtained at the three sites is considered to more than outweigh any limitations associated with lack of replication.

11.2 Role of herbivory on coral reefs of the Saudi Arabian Gulf coast

It has been repeatedly established by field experiments that the process of herbivory on coral reefs reduces algal biomass and influences community structure (see review in Chapter 2). The manipulative experiments described in the present study are no exception and have clearly demonstrated that herbivorous communities play critical roles in regulating benthic algal communities on Saudi Arabian Gulf reefs.

For example, the total exclusion of herbivores (Chapter 6) indirectly revealed how much algal biomass is removed by grazing fish and urchins, and consequently the level of productivity entering the trophic food web. It was concluded that the algal community at the offshore shallow site is inhibited mostly by grazing herbivores because it generated the largest standing crop after exclusion. Furthermore, the fact that algal growth was not equivalent between the three study sites implied that other factors (i.e. abiotic conditions, such as irradiance and nutrient levels) were limiting algal productivity in addition to grazing pressure.

It is well documented that disturbance or biomass removal, such as grazing intensity, cause shifts in the composition and structure of benthic algal communities (Steneck, 1988; Hixon and Brostoff, 1996). Under increasing levels of disturbance, these studies have shown that the community composition will shift towards those taxa which are most perturbation resistant (i.e. macrophyte - filamentous - crustose forms) (Steneck, 1988). Hence the standing crop and composition of an algal community ultimately reflect the current balance between its rate of biomass production and rate of biomass removal, (Steneck, 1988; Steneck and Dethier, 1994). For example, crustose-dominated communities are characteristic of disturbed conditions, such as scouring in areas of high wave exposure, and grazer impact from scraping and excavating herbivores (i.e. parrotfish and echinoids); they are also associated with reduced light penetration at deeper depths (Steneck and Dethier, 1994).

In the present study, comparison of the algal communities growing on the settlement plates that were accessible to all herbivores revealed fundamental differences between each site (Chapter 5). The inshore communities were predominantly covered by filamentous algal forms, while the offshore algal communities were comprised mainly of encrusting forms. If scouring was mainly responsible for the presence of the crustose forms, greater algal cover would have been expected at the inshore site as it experienced the highest level of wave action (Chapters 3 & 4). Hence the predominance of crustose forms at the offshore sites was probably due to the relatively higher grazing pressure.

The composition of the herbivorous communities at each study site (Chapter 8) supports these assertions. For example, the herbivorous fish community at the shallow offshore site was dominated by parrotfish, classified as scraping/excavating grazers (Steneck, 1988). In addition to echinoids, parrotfish are the most effective group of herbivores found on coral reefs (Hixon, 1997). Furthermore,

the apparent absence of any echinoids at the shallow offshore site implied that herbivorous fish were also entirely responsible for the maintenance of the crustose-dominated algal community found there.

Evidence that excavating/scraping herbivores (i.e. parrotfish) regulate the algal community, limit the algal standing crop and so produce a crustose-dominated community observed at the shallow offshore study site was also demonstrated unequivocally at the inshore study site (Plate 11.1). Some settlement plates at the inshore study site were observed to receive increased attention from small groups of visiting parrotfish (*Scarus persicus*) and therefore experienced increased grazing pressure. Parrotfish are known to select preferred feeding areas (Horn, 1989; Bellwood, 1995), but such preferential feeding behaviour may have also been due to visual cues from the equipment deployed (see Chapter 5). It can be seen that increased grazing by the parrotfish on some settlement plates at the inshore site induced a shift in algal community composition towards that found on settlement plates at the offshore study sites (Plate 11.1).

However, such incursions by parrotfish on the inshore reef site were rare as the herbivorous fish community was comprised mainly of *Siganus* spp. Rabbitfish are regarded as herbivores of intermediate grazing intensity, being able to remove algal biomass but not excavate the substratum, and therefore unable to entirely remove algal thalli from cryptic microhabitats and crevices amongst the reef substrata. Thus, evidence of the inshore community being dominated by filamentous algae was supported by the herbivorous fish community comprising mainly grazers of intermediate effectiveness. Interestingly, the inshore reef also supported a large population of *Echinometra mathaei*, again an important scraping/excavating herbivore, yet it was apparently insufficient to further influence the overall grazing pressure and composition of the algal community. This was probably due to its slow movement and manoeuvrability. However, intense localised grazing pressure of this echinoid produced considerable variability in the algal communities (Plates 6.21 and 11.2).

The herbivorous fish community at the deep offshore site was dominated by damselfish, which are classified as non-denuding herbivores and consequently the least effective at removing algal biomass. However, this site also supported a crustose-dominated, low standing crop community compared to the inshore site. This probably results from a combination of grazing pressure from *Diadema setosum*, and possible limitation of algal productivity due to environmental factors such as reduced light penetration.

Overall, the dominant algal forms correlated with the herbivorous community composition and their associated grazing effectiveness. For example, parrotfish at the offshore shallow site exerted a high grazing pressure and promoted crustose forms. In contrast, at the inshore site, despite a seasonally high density of rabbitfish and echinoids, the grazing pressure was sufficient to suppress the growth of macrophytes, but not intense enough to exclude filamentous forms.

However, unlike the reefs in tropical regions such as the Caribbean and Indo-Pacific, Saudi Arabian Gulf reefs experience severe seasonal extremes in environmental conditions, particularly in inshore areas (Chapter 4). Thus, while during summer the observed regulatory impacts of herbivores on algal communities seem comparable with herbivorous interactions documented elsewhere, the winter months were characterised by different communities and relationships.

At the inshore reef site in particular, the algal community underwent a marked seasonal succession characterised by blooms of the macroalgae *Hincksia mitchellae*, *Colpomenia sinuosa* and *Sargassum spp.* (Chapter 5; Figure 5.11). Such extreme seasonality was less apparent amongst the offshore communities, although stands of *Turbinaria* sp. were sometimes observed in cryptic areas at the shallow offshore site. Thus at least during winter, the greater seasonal growth at the inshore site would seem to counter an earlier conclusion (based on the exclusion experiments) that the shallow offshore site experiences greatest algal growth. In addition, the temperature-induced mortality and/or almost total disappearance of herbivorous fish from the inshore reefs, and therefore reduced grazing pressure, probably contributed to the observed seasonal profusion of macroalgae. In contrast, the less severe environmental conditions and therefore higher survivorship of herbivores at the offshore reefs may have prevented an abundant seasonal growth of macroalgae (pers. obs.). Similar trends have been reported from other studies in the region (Basson *et al.*, 1977; Coles, 1988; Sheppard *et al.*, 1992). At present the extent to which seasonal macroalgal blooms are solely influenced by either abiotic conditions (i.e. temperature and nutrients), or herbivore abundance, or a combination of both remains unclear (Johannes *et al.*, 1983; Coles, 1988).

Hence herbivory is an important force in regulating the composition of the algal community, particularly on the offshore reefs. This has important implications for both the maintenance of high primary productivity rates and its transfer throughout the trophic webs, as well as the amelioration of competitive interactions between the benthic algae and other sessile organisms, such as corals (see Chapter 2). However the extent of this influence is markedly seasonal. During winter, abiotic conditions stimulate algal growth to a level that greatly exceeds algal removal by herbivores. In contrast, during summer the absence of seasonal macroalgae, combined with a greater abundance of herbivores, leads to lower algal biomass.

The grazing activities of herbivores have other secondary effects, the most important of which is bioerosion (Hutchings, 1986; Glynn, 1996). The present study originally aimed to compare the bioerosive impact of different herbivore groups at apparent sites (inshore and offshore reefs). Logistical constraints prevented such an extensive survey, but a seasonal estimate of the bioerosive rate (Chapter 9) and foraging behaviour (Chapter 10) was conducted for *E. mathaei* at the inshore study site. The urchin population was apparently not limited by predation, due to the lack of any recorded predation events and the fact that most individuals exhibited exposed foraging behaviour and a low frequency of agonistic behaviour to conspecifics. Furthermore, the large test size of the average

individual compared with other studies on *E. mathaei* (Downing and El-Zahr, 1987; Bak, 1990; McClanahan and Kurtis, 1991), is indicative of old individuals and/or non-limiting food resources. However, given these conditions and without any obvious source of regulation, it is unclear why the population density recorded at the inshore site (mean of 6.5 individuals m^{-2}) was not higher. Downing and El-Zahr (1987) observed higher densities (c. 30 individuals m^{-2}) on fringing reefs around Kuwaiti offshore islands, where average test size was comparatively smaller perhaps due to food-limiting effects. The observed differences may be due to a combination of biophysical factors and natural variability.

Bioerosion rates, determined from gut evacuation of calcium carbonate, did not vary between summer and winter, despite seasonal differences in gut fullness and foraging behaviour. Estimated rates were comparable with those from other studies on *E. mathaei*, given differences in population density and test size (Downing and El-Zahr 1987; Bak, 1990; 1994; McClanahan and Kurtis, 1991). However in the present study, no estimate of the proportion of re-worked material in the gut contents was made. In regions where seasonally high levels of sedimentation occur, such as the Arabian Gulf and particularly at the inshore study site (Chapter 4), the proportion could be considerable. Hence although the evacuation rate of reef material did not vary between seasons, there might have been seasonal differences in the actual ingestion of freshly eroded substratum. Thus it is probable that the bioerosion rates determined were over-estimates, particularly during winter. It is recommended, therefore, that any future study of echinoid bioerosion includes not only estimates of the amount of re-worked material being ingested, particularly in sediment-impacted areas, but also seasonal measurements. Otherwise temporal extrapolations of the bioerosive impact of grazing echinoids and the carbonate budget of a reef community may produce flawed calculations and predictions of overall reef growth or degradation (Bak, 1990; Eakin, 1996). The majority of reefs in the Arabian Gulf are probably not accreting (e.g. the inshore study site), merely supporting scattered coral colonies on ancient Holocene limestone platforms (Sheppard *et al.*, 1992). Only true coral cays, such as the fringing reefs around the Saudi Arabian islands (e.g. the offshore study sites), are examples of accreting reefs in the Gulf (Sheppard *et al.*, 1992). However, to date, no accurate measurements of coral calcification and reef accretion rates are available for the Gulf region. Consequently, assessment of current reef growth or degradation rates and future integrity are not possible.

In summary, it is clear from the results of the present study that the process of herbivory strongly influences marine communities of the Saudi Arabian Gulf's inshore and offshore reefs.

11.3 Importance of herbivory to reef management

The herbivorous community on Saudi Arabian Gulf coral reefs greatly influences reef health and integrity. Management of any exploitative activities (i.e. fishing) that regulate herbivorous communities and their bioerosive impacts should therefore be of paramount importance. The present research was

carried out in an area now designated as a marine reserve, the Jubail Marine Wildlife Sanctuary (JMWS). This area was originally the focus of the joint European Commission (EC) and National Commission for Wildlife Conservation and Development (NCWCD) project, 'Wildlife Sanctuary for the Gulf Region' (Krupp *et al.*, 1996). Results of this study will be added to their knowledge base and be available to the Sanctuary's managers and marine biologists. The establishment of the reserve was prompted by environmental damage caused by the 1991 Gulf War oil spill, which highlighted the vulnerability of marine habitats along the Saudi coastline (Price and Sheppard, 1991; Downing and Roberts, 1993; Roberts *et al.*, 1993). Pollution, such as oil spills and eutrophication, is one of the three most important threats to coral reefs ecosystems, the others being sedimentation and overfishing (Roberts, 1993b). Coastal development within and around the boundaries of the JMWS is managed. Hence sedimentation impacts from land-filling and eutrophication (i.e. from sewage outfalls) should be minimal, as the coastline of the reserve is currently sparsely populated, mainly by fishermen. Apart from the risk of oil spills, the only immediate threats to the coral reefs in the area, particularly the offshore islands, are the impacts of overfishing (Esseen, 1994; Bridson, 1995; Esseen, 1996).

11.3.1 Effects of overfishing

The effects of fishing and the dangers of over-exploitation of reef fisheries is an expanding area of coral reef science. Various studies and reviews have highlighted the impacts (Russ and Alcala, 1989; Jennings *et al.*, 1995; Roberts, 1995a; Jennings and Polunin, 1996) and possible management strategies (Roberts and Polunin, 1991; 1993; Jennings and Polunin, 1996). Recent discoveries and current status of knowledge have been extensively reviewed by Polunin and Roberts (1996).

The principal effects of fishing are well known (Jennings and Lock, 1996). Firstly, fishing obviously causes a reduction in the number of individuals, the extent of which depends on the level of fishing pressure. It can range from local depletion of target species (mainly piscivores) up to global extinction of species vulnerable to capture. Secondly, the removal of fish numbers imposes selective pressures to the fish stock, influencing size composition, life history traits and genetic variability. Finally intense overfishing can occur, known as 'Malthusian overfishing', where the fish stock has been depleted beyond the point of recovery (Pauly *et al.*, 1989).

As previously described (see Chapter 2), numerous studies have demonstrated that exclusion or removal of herbivores releases the algal community from herbivory, causing subsequent profusion of algal biomass and shift in the composition and productivity of the benthic community. Hence in addition to the direct effects on the fished population, overfishing of the herbivorous community has the potential to dramatically impact upon other communities and processes of the reef ecosystem.

While the consequences of overfishing of herbivores on community structure have not been well documented, the effects of the widespread *loss* of a dominant herbivorous group is now well known.

The example of mass mortality of the grazing echinoid, *D. Antillarum*, and subsequent changes in benthic communities in the Caribbean was described in Chapter 2. In this instance, dramatic shifts in benthic community composition and productivity probably heralded the arrival of alternate stable ecosystems (Knowlton, 1992). The continued absence of a dominant herbivore means that Caribbean reefs may never be able to re-attain their pre-mortality existence (Lessios, 1995). Other examples of urchin mortality and loss of herbivorous grazing pressure have also been recorded. One example is the mortality of *E. mathaei* in Japan due to extreme temperatures (Tsuchiya *et al.*, 1987).

However, it is now widely suspected that regions in the Caribbean that had supported large populations of *D. antillarum* were due to overfishing effects, as the stocks of their natural predators were over-exploited (Hay, 1984a). Hence the reverse scenario is also possible, where the herbivorous community is impacted through the overfishing of their predators and, due to the reduced predation pressure, urchin population densities increase to unsustainable levels. For example, *E. mathaei* is the dominant herbivorous echinoid on Kenyan coral reefs (McClanahan and Obura, 1995). McClanahan (1988) demonstrated that *E. mathaei* was competitively superior within the echinoid guild found on Kenyan reefs and that their coexistence was mediated by predation. McClanahan and Muthiga (1989) concurred that reefs supporting larger urchin populations were exposed to reduced predation pressure. Furthermore, there was a correlation between urchin density and fishing pressure (Muthiga and McClanahan, 1987; McClanahan and Muthiga, 1988). Hence it became clear that fishing activities were depleting finfish predators of *E. mathaei*, namely triggerfish (McClanahan, 1990). Reduced predation allowed the echinoids to dominate the reef community (McClanahan and Shafir, 1990). This was particularly apparent on those reefs experiencing intensive overfishing. These areas supported unregulated and expanding populations of *E. mathaei*, which imposed increasing bioerosive pressure on the reef framework and ultimately caused widespread degradation (Muthiga and McClanahan, 1987; McClanahan and Kurtis, 1991).

Hence overfishing of reef fisheries and its impact on the herbivorous community can potentially give rise to two extreme situations. Firstly where the herbivorous community has itself been overfished leading to an increase in benthic algae; or secondly, the removal of herbivore predators which results in their increase and possible habitat degradation due to over-grazing.

11.3.2 Management strategies and the importance of reserves

A wealth of management strategies have been developed for reef fisheries, either for stock assessment, maximising stock yields or maintaining socio-economic expectations, and are usually case-specific (Russ, 1991; Adams, 1996; McManus, 1996). However, it is clear that many conventional methods are not appropriate to tropical reef fisheries; they typically require too much biological information and are too expensive and difficult to enforce (Roberts and Polunin, 1993). Jennings and Polunin (1996) state that favoured strategies currently include; selective cropping of predatory species to increase the yields

of harvested prey species, treating reefs as aggregating devices and harvesting a diverse range of species from all trophic groups (i.e. to prevent over-exploitation of one particular species and maintain the overall community structure). However, Jennings and Polunin (1996) point out that all the above assume use of non-destructive fishing methods.

Alternatively, researchers have been developing hypothetical models of reef ecosystems and fisheries, in order to determine the best fishing strategy that not only maximises stock yields, but also maintains stock size and ensures the protection of the reef habitat and community structure (Polovina, 1984; Atkinson and Grigg, 1984; Grigg *et al.*, 1984; Appeldoorn, 1996). For example, McClanahan (1992) produced a model of a simple reef community involving competing herbivores and demonstrated how urchins could competitively exclude herbivorous fish and attain a maximum biomass at least one order of magnitude higher than their competitors. The lower respiration and consumption rate of urchins means that they can maintain higher biomass at lower resource levels (i.e. algal cover). Hence, if the urchin population is released from regulation, such as by a reduction of predators, then herbivorous fish will be out-competed and eventually excluded due to the urchins reducing the algal resources to levels below which the competing fish can survive. This situation has been observed in natural systems (Hay and Taylor, 1985; McClanahan, 1988, McClanahan and Shafir, 1990). Hence the conclusions of the model are validated.

Having developed a generalised model for the reef community, hypothetical fishing strategies can be applied and their impact on the community monitored. McClanahan (1995) discovered that removal of all fish groups resulted in a dominance by urchins, due to predator removal, and ultimately a low fisheries yield. Fishing only piscivores also produced a low yield, but promoted reef accretion due to the release of corals from competition with benthic algae (i.e. unfished herbivores reduced algal cover). The best strategy, producing the highest yields, involved selectively fishing both piscivores and herbivorous fish, but leaving urchin predators to regulate the urchin population. However, overfishing of the herbivorous fish would lead to increased algal cover and reduced reef accretion by corals. Clearly, the development of models is an important tool in understanding the reef community and testing the effects of different fishing strategies.

An alternative management strategy that has gained popularity over the years is the formation of marine reserves or 'no take' fishing areas. The advantages of a marine reserve over conventional management strategies are that they require minimum biological information and are easy to enforce (Roberts and Polunin, 1991; 1993). Other properties include the increase in abundance and average size of catch species and the protection of spawning stock (Roberts, 1995b). However, conclusive data are still lacking on whether reserves aid the replenishment of unprotected areas through emigration, larval dispersal and recruitment (Roberts and Polunin, 1993).

Reef corals and associated communities of the Arabian Gulf exist in environmental conditions that seasonally reach, and even exceed, the limits of their tolerance, which can cause mortality. As a consequence, the reefs are characterised by low species diversity, but still harbour the key representatives of coral reef flora and fauna. The results of the present study in the Gulf have clearly demonstrated the importance of herbivory in regulating benthic algae and community structure, and influencing reef stability. These effects range from the reduction of algal biomass and the maintenance of algal diversity, to the architectural effects of bioerosion.

Reefs and surrounding habitats in the Gulf support important natural resources that require protection and management. The formation of the JMWS, which encompasses the three sites investigated in the present study, is a valuable measure. Results from the present study have improved understanding of the reef communities and processes. It is hoped that these considerations can be integrated to management strategies of the JMWS and other regions of the Gulf.

Plate 11.1: Settlement plates from the inshore and offshore study sites, from left to right; Jana (shallow) and Jana (deep) (top row), Abu Ali (bottom row). While the left hand plate from Abu Ali is dominated by filamentous algae and sediment, the right hand plate supports a higher coverage of crustose forms and is comparatively similar to the offshore plates (12/8/94).

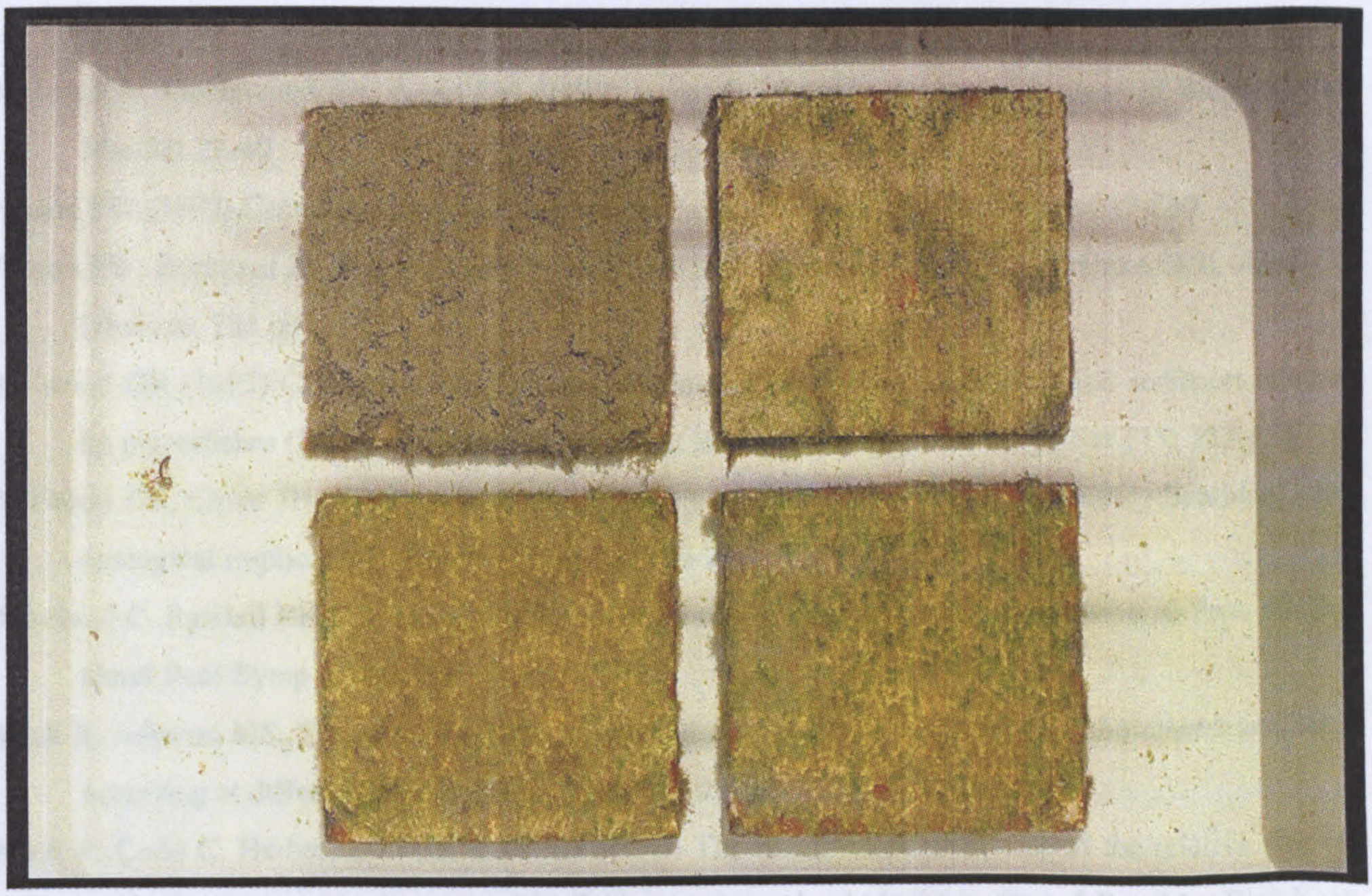


Plate 11.2: Settlement plates from the inshore study site showing the high variability in the algal communities that have developed under the same grazing regimes (i.e. accessible to all herbivores) (7/9/94).

References

Adams TJH (1996) Modern institutional framework for reef fisheries management. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 337-360

Adey WH, Steneck RS (1985) Highly productive Eastern Caribbean reefs: synergistic effects of biological, chemical, physical and geological factors. In: Reaka ML (ed) The ecology of coral reefs. NOAA Undersea Res. Progr., Rockville (Symp Ser Undersea Res, vol 1, pp 163-187)

Appeldoorn RS (1996) Model and method in reef fishery assessment. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 219-248

Atkinson MJ Grigg RW (1984) Model of a coral reef ecosystem. II Gross and net benthic primary productivity production at French Frigate Shoals, Hawaii. Coral Reefs 3: 13-22

Bak RPM, Carpay MJE, de Ruyter van Steveninck ED (1984) Densities of the sea *urchin Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. Mar Ecol Prog Ser 17: 105-108

Bak RPM (1990) Patterns of echinoid bioerosion in two Pacific coral reef lagoons. Mar Ecol Prog Ser 66: 267-272

Basson PW (1979a) Marine algae of the Arabian Gulf coast of Saudi Arabia (first half). Bot Mar 22: 47-64

Basson PW (1979b) Marine algae of the Arabian Gulf coast of Saudi Arabia (second half). Bot Mar 22: 65-82

Basson PW, Mohammed SA, Arora DK (1989) A survey of the benthic marine algae of Bahrain. Bot Mar 32: 27-40

Basson PW (1992) Checklist of marine algae of the Arabian Gulf. J Uni Kuwait 19: 217-230

Basson PW, Burchard JE, Hardy JT, Price ARG (1977) Biotopes of the western Arabian Gulf. Aramco, Dhahran, 284 pp

Bellwood DR (1995) Carbonate transport and within-reef patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. Mar Ecol Prog Ser 117: 127-136

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Env Biol Fish 28: 189-214

Birkeland C, Randall RH (1981) Facilitation of coral recruitment by echinoid excavations. Proc 4th Int Coral Reef Symp 1: 695-698

Black R, Johnson MS, Trendall JT (1982) Relative size of Aristotle's Lantern in *Echinometra mathaei* occurring at different densities. Mar Biol 71: 101-106

Black R, Codd C, Herbert D, Vink S, Burt J (1984) The functional significance of the relative size of Aristotle's Lantern in the sea urchin *Echinometra mathaei* (de Blainville). J Exp Mar Biol Ecol 77: 81-97

Borowitzka MA (1981) Algae and grazing in coral reef ecosystems. Endeavour 5: 99-106

Borowitzka MA (1983) Calcium carbonate deposition by reef algae: morphological and physiological aspects. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 16-27

Brawley SH, Adey WH (1977) Territorial behaviour of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Env Biol Fish 2: 45-51

Brawley SH, Adey WH (1981) The effects of micrograzers on algal community structure in a coral reef microcosm. Mar Biol 61: 167-177

Breitburg DL (1985) Development of a subtidal benthic community: factors affecting species compositions and the mechanisms of succession. Oecologia 65: 173:184

Bridson P (1995) Sanctuary fisheries survey. In: Feltkamp E, Krupp F (eds) Establishment of a marine habitat and wildlife sanctuary for the Gulf region: Final report for Phase III. Frankfurt, pp 183-204

Brock RE (1979) An experimental study on the effect of grazing by parrotfishes and the role of refuges in the benthic community structure. Mar Biol 51: 381-388

Burchard JE (1979) Coral fauna of the Arabian Gulf. Aramco, Dhahran, 36pp

Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. J Mar Res 39: 749-765

Carpenter RC (1983) Differential effects of coral reef herbivores on algal community structure and function. In: Reaka ML (ed) The ecology of deep and shallow coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 1, pp 111-118)

Carpenter RC (1984) Predator and population density control of homing behaviour in the Caribbean echinoid *Diadema antillarum*. Mar Biol 82: 101-108

Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56: 345-363

Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proc Natl Acad Sci 85: 511-514

Carpenter RC (1990a) Mass mortality of *Diadema antillarum*: I Long-term effects on sea urchin population-dynamics and coral reef algal communities. Mar Biol 104: 67-78

Carpenter RC (1990b) Mass mortality of *Diadema antillarum*: II Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Mar Biol 104: 79-86

Carpenter RC (1997) Invertebrate predators and grazers. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 198-229

Carpenter RC, Williams SL (1993) Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol Oceanogr 38: 687-694

Carpenter RC, Hackney JM, Adey WH (1991) Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol Oceanogr 36: 40-49

Chalker BE (1983) Calcification by corals and other animals on the reef. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 29-45

*Choat JH (1983) Estimation of the abundances of herbivorous fishes and their grazing rates within reef systems. In: Baker JT, Carter RM, Sammarco PW, Stark KP (eds) Proceedings of the Inauguree Conference, Townsville, Great Barrier Reef 1983. JCU, Townsville pp 171-177

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, London, pp 120-153

Clarke MWH, Keij AJ (1973) Organisms as producers of carbonate sediment and indicators of environment in the southern Persian Gulf. In: Purser BH (ed) The Persian Gulf. Springer-Verlag, New York, pp 32-56

Coles SL (1988) Limitations on reef coral development in the Arabian Gulf: temperature or algal competition? Proc 6th Int Coral Reef Symp 3: 211-216

Coles SL, McCain JC (1990) Environmental factors affecting benthic infaunal communities of the western Arabian Gulf. Mar Env Res 29: 289-315

Coles SL, Tarr AB (1990) Reef fish assemblages in the western Arabian Gulf: a geographically isolated population in an extreme environment. Bull Mar Sci 47: 696-720

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. Coral Reefs 9: 231-237.

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. Am Nat 111: 1119-1144

Dart JKG (1972) Echinoids, algal lawns and coral re-colonisation. Nature 239: 50-51

Davies PJ (1983) Reef growth. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 69-106

De Clerck O, Coppejans E (1994) Status of the macroalgae and seagrass vegetation after the 1991 Gulf War oil spill. Courier Forschungsinstitut Senckenberg 166: 18-21

De Clerck O, Coppejans E (1996) Marine algae of the Jubail Marine Wildlife Sanctuary, Saudi Arabia. In: Krupp F, Abuzinada AH, Nader IA (eds) A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, pp 199-289

de Ridder C, Lawrence JM (1982) Food and feeding mechanisms: echinoidea. In Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema, Rotterdam, pp 57-115

de Ruyter van Steveninck ED, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Mar Ecol Prog Ser 34: 87-94

Dodge RE, Logan A, Antonius A (1982) Quantitative reef assessment studies in Bermuda: a comparison of methods and preliminary results. Bull Mar Sci 32: 745-760

Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, London, pp 261-293

Dotan A (1990) Distribution of regular sea urchins on coral reefs near that south-eastern tip of the Sinai peninsula, Red Sea. Israel J Zool 37: 15-29

Downing N (1985) Coral reef communities in an extreme environment: the northwestern Arabian Gulf. Proc 5th Int Coral Reef Congr 6: 343-348

Downing N, El-Zahr CR (1987) Gut evacuation and filling rates in the rock-boring sea urchin, *Echinometra mathaei*. Bull Mar Sci 41: 579-584

Downing N, Roberts CM (1993) Has the Gulf War affected coral reefs of the northwestern Gulf? Mar Poll Bull 27: 149-156

Downing N, Tubb RA, El-Zahr CR, McClure RE (1985) Artificial reefs in Kuwait, northern Arabian Gulf. Bull Mar Sci 37: 157-178

Duffy JE, Paul VJ (1992) Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes. Oecologia 90: 333-339

Eakin CM (1988) Avoidance of damselfish lawns by the sea urchin Diadema mexicanum at Uva Island, Panamá. 2: 21-26

Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. Coral Reefs 15: 109-119

Esseen M (1994) A survey of the fisheries of the proposed sanctuary area. In: Feltkamp E, Krupp F (eds) Establishment of a marine habitat and wildlife sanctuary for the Gulf region: Final report for Phase II. Frankfurt, pp 559-592

Esseen M (1996) A survey of the fisheries in the Jubail Marine Wildlife Sanctuary. In: Krupp F, Abuzinada AH, Nader IA (eds) A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, pp 459-479

Fadlallah YH, Allen KW, Estudillo RA (1995) Mortality of shallow reef corals in the western Arabian Gulf following aerial exposure in winter. Corals Reefs 14: 99-108

Farrell TM (1989) Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. J Exp Mar Biol Ecol 128: 57-73

Farrell TM (1991) Models and mechanisms of succession: an example from a rocky intertidal community. Ecol Monogr 61: 95-113

Foster SA (1987) The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. J Exp Mar Biol Ecol 105: 1-20

Frydl P, Stearn CW (1978) Rate of bioerosion by parrotfish in Barbados reef environments. J Sediment Petrol 48: 1149-1157

Glynn PW (1990) Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. In: Dubinsky Z (ed) Ecosystems of the world. Vol. 25: Coral reefs. Elsevier Scientific Publications, pp 365-400

Glynn PW (1997) Bioerosion and coral-reef growth: a dynamic balance. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 198-229

Glynn PW, Wellington GM, Birkeland C (1979) Coral reef growth in the Galapagos: limitation by sea urchins. Science 203: 47-49.

Grigg RW, Polovina JJ, Atkinson MJ (1984) Model of a coral reef ecosystem. III Resource limitation, community regulation, fisheries yield and resource management. Coral Reefs 3: 23-27

Grünbaum H, Bergman G, Abbot DP, Ogden JC (1978) Intraspecific agonistic behaviour of the rock-boring sea urchin *Echinometra lucunter* (L.) (Echinodermata: Echinoidea). Bull Mar Sci 28: 181-188.

Hart LJ, Chia F-S (1990) Effect of food supply and body size on the foraging behaviour of the burrowing sea urchin *Echinometra mathaei* (de Blainville). J Exp Mar Bio Ecol 135: 99-108

Hatcher BG (1981) The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Proc 4th Int Coral Reef Symp 2: 515-524

Hatcher BG, (1983) Grazing in coral reef ecosystems. In: Barnes DJ (ed) Perspectives on coral reefs. Aust. Inst. Mar. Sci., Townsville, pp 164-179

Hatcher BG (1988) Coral reef primary productivity: a beggar's banquet. Trends Ecol Evol 3: 106-111

Hatcher BG (1990) Coral reef primary productivity: a hierarchy of pattern and process. Trends Ecol Evol 5: 149-155

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Biol Ecol 69: 61-84

Hawkins CM, Lewis JB (1982) Ecological energetics of the tropical seas urchin Diadema antillarum Philippi in Barbados, West Indies. Est. Coast. Shelf Sci. 15: 645-669

Hay ME (1981a) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquatic Botany 11: 97-109

Hay ME (1981b) Herbivory, algal distribution and the maintenance of between-habitat diversity on a tropical fringing reef. Amer Nat 118: 520-540

Hay ME (1984a) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65: 446-454

Hay ME (1984b) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities. Oecologia 64: 396-407

Hay ME, Goertemiller T (1983) Between habitat differences in herbivore impact on Caribbean coral reefs. In: Reaka ML (ed) The ecology of deep and shallow coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 1, pp 97-102)

Hay ME, Taylor PR (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia 65: 591-598

Hay ME, Colburn T, Downing D (1983) Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. Oecologia 58: 299-308

Hay M, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification and plant quality. Ecology 75: 1714-1726

Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30: 65-127

Highsmith RC, Lueptow RL, Schonberg SC (1983) Growth and bioerosion of three massive corals on the Belize barrier reef. Mar Ecol Prog Ser 13: 261-271

Hixon MA (1983) Fish grazing and community structure of reef corals and algae: a synthesis of recent studies. In: Reaka ML (ed) The ecology of deep and shallow coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 1, pp 79-87)

Hixon MA (1985) Overview: coral reef community structure and function. In: Reaka ML (ed) The ecology of coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 3, pp 27-32)

Hixon MA (1997) Effects of reef fishes on corals and algae. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 230-248

Hixon MA Brostoff WN (1981) Fish grazing and community structure of Hawaiian reef algae. Proc 4th Int Coral Reef Symp 2: 507-514

Hixon MA, Brostoff WN (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220: 511-513.

Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol Monogr 66: 67-90

Horn MH (1989) Biology of marine herbivorous fishes. Oceanogr Mar Biol Annu Rev 27: 167-272

Hoskin CM, Reed JK (1985) Carbonate sediment production by the rock-boring urchin *Echinometra lucunter* and associated endolithic infauna at Black Rock, Little Bahama Bank. In: Reaka ML (ed) The ecology of coral reefs. NOAA Undersea Res. Progr., Rockville (Symp Ser Undersea Res, vol 1, pp 151-161)

*Hudson JH (1977) Long-term bioerosion rates on a Florida reef: new method. Proc 3rd Int Coral Reef Symp 2: 491-498

Hughes TP, Keller BD, Jackson JBC, Boyle MJ (1985) Mass mortality of the *echinoid Diadema antillarum* Philippi in Jamaica. Bull Mar Sci 36: 377-384

Hughes TP, Reed DC, Boyle M-J (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. J Exp Mar Biol Ecol 113: 39-59

Hunte W, Youngalo D (1988) Recruitment and population recovery of Diadema antillarum (Echinodermata; Echinoidea) in Barbados. Mar Ecol Prog Ser 45: 109-119

Hunte W, Côte I, Tomascik T (1986) On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. Coral Reefs 4: 135-139

Hunter JR (1986) The physical oceanography of the Arabian Gulf: a review and theoretical interpretation of previous observations. In: Halwagy R, *et al.* (eds) First Gulf Conference on Environment and Pollution, Kuwait, 1982. University of Kuwait, pp 1-23

Hutchings PA (1986) Biological destruction of coral reefs: a review. Coral Reefs 4: 239-252

Hutchings PA, Bamber L (1985) Variability of bioerosion rates at Lizard Island, Great Barrier Reef: preliminary attempts to explain these rates and their significance. Proc 5th Int Coral Reef Symp 5: 333-338

Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 193-218

Jennings S, Polunin NVC (1996) Impacts of fishing on tropical reef ecosystems. Ambio 25: 44-49

Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14: 225-236

Johannes RE, Wiebe WJ, Crossland CJ, Rimmer DW, Smith SV (1983) Latitudinal limits of coral reef growth. Mar Ecol Prog Ser 11: 105-111

John VC, Coles SL, Abozed AI (1990) Seasonal cycles of temperature, salinity and water masses of the Western Arabian Gulf. Oceanologia Acta 13: 273-281

Jones DA, Price ARG, Hughes RN (1978) Ecology of the high saline lagoons, Dawhat as Sayh, Arabian Gulf, Saudi Arabia. Est Coast Mar Sci 6: 253-262

Khamala CPM (1971) Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diana Beach, Kenya. Mar Biol 11: 167-172

Kennelly SJ (1983) An experimental approach to the study of factors affecting algal colonisation in a sublittoral kelp forest. J Exp Mar Biol Ecol 68: 257-276

Keough MJ (1983) Patterns of recruitment of sessile invertebrates in two subtidal habitats. J Exp Mar Biol Ecol 66: 213-245

Kiene WE (1985) Biological destruction of experimental coral substrates at Lizard Island, Great Barrier Reef, Australia. Proc 5th Int Coral Reef Symp 5: 339-344

Kiene WE, Hutchings PA (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef. Coral Reefs 13: 91-98

Kinsman DJJ (1964) Reef coral tolerance of high temperatures and salinities. Nature 202: 1280-1282.

Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. J Exp Mar Biol Ecol 131: 1-22

Klumpp DW, Polunin NVC (1989) Partitioning among grazers of food resources within damselfish territories on a coral reef. J Exp Mar Biol Ecol 125: 145-169

Klumpp DW McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. Mar Ecol Prog Ser 86: 77-89

Klumpp DW, McKinnon D, Daniel P (1987) Damselfish territories: zones of high productivity on coral reefs. Mar Ecol Prog Ser 40: 41-51

Knowlton N (1992) Threshold and multiple stable states in coral-reef community dynamics. Am Zool 32: 674-682

Krebs CJ (1989) Ecological methodology. Harper Collins, New York, 654 pp

Krupp F, Müller T (1994) The status of fish populations in the northern Arabian Gulf two years after the 1991 Gulf War oil spill. Courier Forschungsinstitut Senckenberg 166: 67-75

Krupp F, Müller T, Al-Sana'a M, Al-Marri M (1994) Survey of fishes and fish assemblages in Dawhat ad-Dafi al-Musallamiya and the Gulf coral islands. In: Feltkamp E, Krupp F (eds) Establishment of a marine habitat and wildlife sanctuary for the Gulf region: Final report for Phase II. Frankfurt, pp 537-558

Krupp F, Almarri MA (1996) Fishes and fish assemblages of the Jubail Marine Wildlife Sanctuary. In: Krupp F, Abuzinada AH, Nader IA (eds) A marine wildlife sanctuary for the Arabian Gulf.

Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, pp 339-350

Krupp F, Abuzinada AH, Nader IA (1996) A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, 511 pp

Larkum AWD (1983) The primary productivity of plant communities on coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Aust. Inst. Mar. Sci., Townsville, pp 221-230

Lawrence LM, Sammarco PW (1982) Effects of feeding on the environment: echinoidea. In Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema, Rotterdam, pp 499-519

Lessios HA (1988a) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Ann Rev Ecol Syst 19: 371-93

Lessios HA (1988b) Population dynamics of Diadema antillarum (Echinodermata: Echinoidea) following the mass mortality in Panamá. Mar Biol 99: 515-526

Lessios HA (1995) *Diadema antillarum* 10 years after mass mortality: still rare, despite help from a competitor. Proc Roy Soc Lond 259: 331-337

Lessios HA, Robertson DR, Cubit JD (1984a) Spread of *Diadema* mass mortality through the Caribbean. Science 226: 335-337

Lessios HA, Cubit JD, Robertson DR, Shulman MJ, Parker MR, Garrity SD, Levings SC (1984b) Mass mortality of *Diadema antillarum* on the Caribbean coast of Panamá. Corals Reefs 3: 173-182

Levitan DR (1988a) Asynchronous spawning and aggregation behaviour in the sea urchin *Diadema antillarum* (Philippi). In: Burke R et al., (eds) Echinoderm Biology. AA Balkema, Rotterdam, Netherlands. (Proc 6th Int Echinoderm Conference, pp 181-186).

Levitan DR (1988b) Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. Oecologia 76: 627-629

Levitan (1988c) Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. J Exp Mar Ecol Biol 119: 167-178

Levitan DR (1989) Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. Ecology 70: 1414-1424

Levitan DR (1991a) Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. Mar Biol 111: 431-436

Levitan DR (1991b) Influence of body size and population density on fertilisation success and reproductive output in a free-spawning invertebrate. Biol Bull 181: 261-268

Levitan DR, Genovese SJ (1989) Substratum-dependent predator-prey dynamics: patch reefs as refuges from gastropod predation. J Exp Mar Biol Ecol 130: 111-118

Lewis JB (1964) Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. Can J Zool 42: 549-557

Lewis SM (1986) The role of herbivorous fish in the organisation of a Caribbean reef community. Ecol Monogr 56: 183-200

Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. J Exp Mar Biol Ecol 87: 215-228

Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. J Exp Mar Biol Ecol 95: 271-278

Lieske E, Myers RM (1996) Collins' pocket guide. Coral reef fishes: Indo-Pacific and Caribbean. Harper-Collins, London, 400 pp

Littler MM, Taylor PR, Littler DS (1983) Algal resistance to herbivory on a Caribbean Barrier Reef. Coral Reefs 2: 111-118

Lobel PS (1980) Herbivory by damselfish and their role in coral reef community ecology. Bull Mar Sci 30: 273-289

Marshall JF (1983) Marine lithification in coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 231-239

Marshall JF, Davies PJ (1982) Internal structure and Holocene evolution of One Tree Reef, southern Great Barrier Reef. Coral Reefs 1: 21-29

Martin-Smith KM (1992) Seasonal variation in tropical benthic Sargassum and associated motile epifauna. Proc 7th Int Coral Reef Symp 2: 881-886

McCain JC, Tarr AB, Carpenter KE, Coles SL (1984) Marine ecology of Saudi Arabia. A survey of coral reefs and reef fishes in the northern area, Arabian Gulf, Saudi Arabia. Fauna of Saudi Arabia 6: 102-126

McClanahan TR (1988) Coexistence in a sea urchin guild and its implications to coral diversity and degradation. Oecologia 77: 210-218

McClanahan TR (1990) Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. Env Biol Fish 43: 187-193

McClanahan TR (1992) Resource utilisation, competition and predation: a model and example from coral reef grazers. Ecological Modelling 61: 195-215

McClanahan TR (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecological Modelling 80: 1-19

McClanahan TR, Muthiga NR (1988) Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia 166: 269-276

McClanahan TR, Muthiga NA (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. J Exp Mar Biol Ecol 126: 77-94

McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchins abundance and diversity in Kenyan coral reef lagoons. Oecologia 83: 362-370

McClanahan TR, Kurtis JD (1991) Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). J Exp Mar Biol Ecol 147: 121-146

McClanahan TR, Obura D (1995) Status of Kenyan coral reefs. Coastal Management 23: 57-76

McCook LJ, Chapman ARO (1991) Community succession following massive ice-scour on an exposed rocky shore: effects of *Fucus* canopy algae and of mussels during late succession. J Exp Mar Biol Ecol 154: 137-169

McCook LJ, Chapman ARO (1993) Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. Mar Biol 115: 565-575

McLean RF (1967) Measurements of beachrock erosion by some tropical marine gastropods. Bull Mar Sci 17:551-561

McManus JW (1996) Social and economic aspects of reef fisheries and their management. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 249-282

Miller AC (1982) Effects of differential fish grazing on the community structure of an intertidal reef flat at Enewetak Atoll, Marshall Islands. Pacific Science 36: 467-482

Montgomery WL (1980) Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. J Exp Mar Biol Ecol 47: 9-24

Montgomery WL, Gerrodette T, Marshall LD (1980) Effects of grazing by the yellowtail surgeonfish, *Prionurus punctatus*, on algal communities in the Gulf of California, Mexico. Bull Mar Sci 30: 901-908

Montgomery WL, Myrberg AA, Fishelson L (1989) Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to Acanthurus nigrofuscus (Forsskal). J Exp Mar Biol Ecol 132: 179-207

Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69: 1367-1382

Muthiga NA, McClanahan TR (1987) Populations changes of a sea urchin (*Echinometra mathaei*) on an exploited fringing reef. Afr J Ecol 25: 1-8

Neill JB (1988) Experimental analysis of burrow defence in *Echinometra mathaei* (de Blainville) on an Indo-West Pacific reef flat. J Exp Mar Biol Ecol 115: 127-136

Nelson SG, Tsutsui RN (1981) Browsing by herbivorous reef-fishes on the agarophyte Gracilaria edulis (Rhodophyta) at Guam, Mariana islands. Proc 4th Int Coral Reef Symp 2: 503-506

Nelson SG, Chiang Y-M (1992) An exploratory analysis of the food habits of herbivorous surgeonfishes (Acanthuridae) from French Polynesia. Proc 7th Int Coral Reef Symp 2: 920-926

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampa*. Limnol Oceanogr 11: 92-108

Ochavillo DG, Dixon PI, Aliño PM (1992) The daily food ration of parrotfishes in the fringing reefs of Bolinao, Pangasinan, northwestern Philippines. Proc 7th Int Coral Reef Symp 2: 927-933

Ogden JC (1977) Carbonate sediment production by parrotfish and sea urchins on Caribbean reefs. In Frost SH, Weiss MP, Saunders JB (eds) Reefs and related carbonates - ecology and sedimentology. Am Assoc Petrol Geol Stud Geol 4: 281-288

Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. Env Biol Fish 3: 49-63

Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* (Philippi): formation of halos around West Indian patch reefs. Science 182: 715-717

Osman RW (1978) The influence of seasonality and stability on the species equilibrium. Ecology 59: 383-399

Paine RT (1966) Food web complexity and species diversity. Am Nat 100: 65-75

*Pauly D, Silvestre G, Smith IR (1989) On development, fisheries and dynamite: a brief review of tropical fisheries management. Nat Resour Modelling 3: 307-329

Pearse JS, Arch SW (1969) The aggregation behaviour of *Diadema* (Echinodermata, Echinoidea). Micronesica 5: 165-171

Polovina JJ (1984) Model of a coral reef ecosystem. I The Ecopath model and its application to French Frigate Shoals. Coral Reefs 3: 1-11

*Polovina JJ (1991) Fisheries applications and biological impacts of artificial reefs. In: Seaman W, Sprague LM (eds) Artificial habitats for marine and freshwater fisheries. Academic Press, San Diego, pp 153-176

Polunin NVC, Roberts CM (1996) Reef fisheries. Chapman and Hall, London, pp 477

Polunin NVC, Harmelin-Vivien M, Galzin R (1995) Contrasts in algal food processing among five herbivorous coral-reef fishes. J Fish Biol 47: 455-465

Price ARG (1981) Studies on the echinoderm fauna of the western Arabian Gulf. J Nat Hist 15: 1-15

Price ARG (1982a) Western Arabian Gulf echinoderms in high salinity waters and the occurrence of dwarfism. J Nat Hist 16: 519-527.

Price ARG (1982b) Echinoderms of Saudi Arabia. Comparison between echinoderm faunas of Arabian Gulf, SE Arabia, Red Sea and Gulf of Aqaba and Suez. Fauna of Saudi Arabia 4: 3-21

Price ARG (1983) Echinoderms of Saudi Arabia. Echinoderms of the Arabian Gulf coast of Saudi Arabia. Fauna of Saudi Arabia 5: 28-108

Price ARG, Sheppard CRC (1991) The Gulf: past, present and possible future states. Mar Poll Bull 22: 222-227

Price ARG, Rezai H (1996) New echinoderm records for the Gulf including Crown-of-Thorns starfish, *Acanthaster planci* (Linnaeus), and their biogeographical significance. Fauna of Saudi Arabia 15: 386-390

Price ARG, Sheppard CRC, Roberts CM (1993) The Gulf: its biological setting. Mar Poll Bull 27: 9-15

Purcell SW, Bellwood DR (1993) A functional analysis of food procurement in two surgeonfish species Acanthurus nigrofuscus and Ctenochaetus striatus (Acanthuridae). Env Biol Fish 37: 139-159

Purser BH, (1973) The Persian Gulf. Springer-Verlag, New York

Randall J E (1961) Overgrazing of algae by herbivorous marine fishes. Ecology 42: 812

Randall JE (1965) Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46: 255-260

Randall JE (1974) The effects of fishes on coral reefs. Proc 2nd Int Coral Reef Symp 1: 159-166

Reinthal PN, Kensley B, Lewis SM (1984) Dietary shifts in the Queen triggerfish *Balistes vetula*, in the absence of its primary food item, *Diadema antillarum*. P S Z N I Mar Ecol 5: 191-195

*Renkonen O (1938) Statisch-okologische Untersuchungen uber die terrestche kaferwelt der finnischen bruchmoore. Ann Zool Soc Bot Fenn Vanamo 6: 1-231

Reynolds RM (1993) Physical oceanography of the Gulf, Strait of Hormuz and the Gulf of Oman: results from the *Mt Mitchell* expedition. Mar Poll Bull 27: 35-60

Richmond MD (1994) Ecological status of the marine subtidal habitats and the effects of the Gulf War oil spill, with special reference to soft-substrata communities. In: Feltkamp E, Krupp F (eds) Establishment of a marine habitat and wildlife sanctuary for the Gulf region: Final report for Phase II. Frankfurt, pp 438-459

Richmond MD (1996) Status of subtidal biotopes of the Jubail Marine Wildlife Sanctuary with special reference to soft-substrata communities. In: Krupp F, Abuzinada AH, Nader IA (eds) A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, pp 159-176

Risk MJ, MacGeachy JK (1978) Aspects of bioerosion of modern Caribbean reefs. Revta Biol Trop 26: 85-105

Roberts CM (1993a) Impact of the Gulf War on the coral reefs of Saudi Arabia: results of the November 1992 survey. Report to the World Conservation Union (IUCN), Gland, 18 pp

Roberts CM (1993b) Coral reefs: health, hazards and history. Trends Ecol Evol 8: 425-727

Roberts CM (1995a) Effects of fishing on the ecosystem structure of coral reefs. Conservation Biology 9: 988-995

Roberts CM (1995b) Rapid build-up of fish biomass in a Caribbean marine reserve. Conservation Biology 9: 815-826

Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser 41: 1-8

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1: 65-91

Roberts CM, Polunin NVC (1993) Marine reserves: simple solutions to managing complex fisheries? Ambio 22: 363-368

Roberts CM, Dawson Sheppard AR, Ormond RFG (1988) The usefulness of butterfly fishes as environmental indicators on coral reefs. Proc 6th Int Coral reef Symp 2: 331-336

Roberts CM, Downing N, Price ARG (1993) Oil on troubled waters: impacts of the Gulf War on coral reefs. In: Ginsburg RN, (ed) Proceedings of the colloquium and forum on global aspects of coral reefs: healths, hazards and history. Rosentiel School of Marine and Atmospheric Sciences, University of Miami, pp 35-41

Robertson DR (1987) Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. Copeia 3: 637-642

Robertson DR (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. Mar Biol 111: 437-444

Robinson CL, Williams AH (1985) A comparison of fore and back reef populations of *Diadema antillarum* Philippi and *Eupomacentrus planifrons* Cuvier at St Croix, US Virgin Islands. In: Reaka ML (ed) The ecology of coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 3, pp 139-149)

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62: 185-202

Russ GR (1984a) Distribution and abundance of herbivorous grazing fishes in the central Great barrier reef. I Levels of variability across the entire continental shelf. Mar Ecol Prog Ser 20: 23-34

Russ GR (1984b) Distribution and abundance of herbivorous grazing fishes in the central Great barrier reef. II Patterns of zonation of mid-shelf and outershelf reefs. Mar Ecol Prog Ser 20: 35-44

Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, New York, pp 601-636

Russ GR, St. John J (1988) Diets, growth rates and secondary production of herbivorous coral reef fishes. Proc 6th Int Coral Reef Symp 2: 37-43

Russ GR, Alcala AC (1989) Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar Ecol Prog Ser 56: 13-27

Russo AR (1977) Water flow and the distribution and abundance of echinoids (Genus *Echinometra*) on an Hawaiian reef. Aust J Mar Freshwater Res 28: 693-702

Russo AR (1980) Bioerosion by two rock-boring echinoids (*Echinometra mathaei* and *Echinostrephus aciculatus*) on Eniwetok Atoll, Marshall Islands. J Mar Res 38: 99-110

Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition and biological disturbance. J Exp Mar Biol Ecol 45: 245-272

Sammarco PW (1982a) Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. J Exp Mar Biol Ecol 65: 83-105

Sammarco PW (1982b) Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J Exp Mar Biol Ecol 61: 31-55

Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I Algal community structure. Mar Ecol Prog Ser 13: 1-14

Sammarco PW, Carleton JH (1981) Damselfish territoriality and coral community structure: reduced grazing, coral recruitment and effects on coral spat. Proc 4th Int Coral Reef Symp 2: 525-535

Sammarco PW, Williams AH (1982) Damselfish territoriality: influence on *Diadema* distribution and implications for coral community structure. Mar Ecol Prog Ser 8: 53-59

Sammarco PW, Levinton JS, Ogden JC (1974) Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J Mar Res 32: 47-53

Scoffin TP, Stearn CW, Boucher D, Frydl P, Hawkins CM, Hunter IG, MacGeachy JK (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados Part II Erosion, sediments and internal structure. Bull Mar Sci 30: 475-508

Scott FJ, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the Great barrier Reef. Mar Ecol Prog Ser 39: 293-304

*Sheppard CRC (1985) Corals, coral reefs and other hard substrate biota of Bahrain. ROPME Marine Habitat Survey Environmental Protection Unit, Bahrain, 25 pp

Sheppard CRC (1988) Similar trends, different causes: responses of corals to stressed environments in Arabian seas. Proc 6th Int Coral Reef Symp 3: 297-301

Sheppard CRC (1993) Physical environment of the Gulf relevant to marine pollution: an overview. Mar Poll Bull 27: 3-8

Sheppard CRC, Sheppard ALS (1991) Corals and coral communities of Arabia. Fauna of Saudi Arabia 12: 3-10

Sheppard CRC, Price ARG (1991) Will marine life survive in the Gulf? New Scientist 1759: 36-40

Sheppard CRC, Price ARG, Roberts CM (1992) Marine ecology of the Arabian region: patterns and processes in extreme tropical environments. Academic Press, London, 359 pp

Shinn EA (1976) Coral reef recovery in Florida and the Persian Gulf. Env Geol 1: 241-254

Shulman MJ (1990) Aggression among sea urchins on Caribbean coral reefs. J Exp Mar Biol Ecol 140: 197-208

Smith GB, Saleh M, Sangoor K (1987) The reef ichthyofauna of Bahrain (Arabian Gulf) with comments on its zoogeographic affinities. Arabian Gulf J Sci Res B5: 127-146

Smith SV (1983) Coral reef calcification. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 240-247

Sousa WP (1979a) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol Monogr 49: 227-254

Sousa WP (1979b) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60: 1225-1239

Stearn CW, Scoffin TP (1977) Carbonate budget of a fringing reef, Barbados. Proc 3rd Int Coral Reef Symp 2: 471-476

Steneck RS (1983) Quantifying herbivory on coral reefs: just scratching the surface and still biting off more than we can chew. In: Reaka ML (ed) The ecology of deep and shallow coral reefs. NOAA, Rockville (Symp Ser Undersea Res, vol 1, pp 103-111)

Steneck RS (1988) Herbivory on coral reefs: a synthesis. Proc 6th Int Coral Reef Symp 1: 37-49.

Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68: 299-319

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. Oikos 69: 476-498

Stephenson W, Searles RB (1960) Experimental studies on the ecology of intertidal environments at Heron Island. Aust J Mar Freshwater Res 11: 241-267

Sutherland JP (1974) Multiple stable points in natural communities. Am Nat 108: 859-873

Sutherland JP, Karlson RH (1977) Development and stability of the fouling community at Beaufort, North Carolina. Ecol Monogr 47: 425-446

Sutton M (1983) Relationships between reef fishes and coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 248-255

Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58: 3-15

Trudgill ST (1983) Measurements of rates of erosion of reefs and reef limestones. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 256-262

Tsuchiya M, Nishihira M (1985) Agonistic behaviour and its effect on the dispersion pattern in two types of the sea urchin *Echinometra mathaei* (de Blainville). Galaxea 4: 37-48

Tsuchiya M, Yanagiya K, Nishihira M (1987) Mass mortality of the sea urchin *Echinometra mathaei* (Blainville) caused by high water temperatures on the reef flats in Okinawa, Japan. Galaxea 6: 375-385

Turner SJ, Todd CD (1993) The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St Andrews Bay, NE Scotland. J Exp Mar Biol Ecol 166: 251-272

Underwood AJ, Anderson MJ (1994) Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. J Mar Biol Ass UK 74: 563-584

Vine PJ (1974) Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. Mar Biol 24: 131-136

Vogt H (1994a) Status of the inshore and offshore coral. In: Feltkamp E, Krupp F (eds) Establishment of a marine habitat and wildlife sanctuary for the Gulf region: Final report for Phase II. Frankfurt, pp 460-494

Vogt H (1994b) Status of the coral reefs after the Gulf. Courier Forschungsinstitut Senckenberg 166: 61-66

Vogt H (1996) Investigations on coral reefs in the Jubail Marine Wildlife Sanctuary using underwater video recordings and digital image analysis. In: Krupp F, Abuzinada AH, Nader IA (eds) A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. Hubert and Co., Göttingen, pp 302-326

Vousden DHP (1988) The Bahrain marine habitat survey. Vol 1. The technical report. ROPME, 103 pp

Wanders JBW (1977) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). III. The significance of grazing. Aquat Bot 3: 357-390

Wilkinson CR (1983) Role of sponges in coral reef structural processes. In: Barnes DJ (ed) Perspectives on coral reefs. Aust Inst Mar Sci, Townsville, pp 263-274

Wilkinson CR, Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. II Nitrogen fixation. Mar Ecol Prog Ser 13: 15-19

Williams AH (1981) An analysis of competitive interactions in a patchy backreef environment. Ecology 62: 1107-1120

Williams SH, Carpenter RC (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. Mar Ecol Prog Ser 47: 145-152

*Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50: 296-302

*Yodzis P (1976) The effects of harvesting on competitive systems. Bull Math Biol 38: 97-109

* cited only

Appendix 1

Abiotic Conditions

Appendix 1.1 Abu Ali

Raw data for the abiotic conditions recorded throughout the study period.

Date	Time	Temp.	Salin.
14/5	12:20	28	
17/5	12:05	28.5	
21/5	12:40	29.5	
24/5	12:55	31	43
29/5	12:20	32.2	41
1/6	12:00	31.8	41
7/6	12:15	29.9	43
12/6	11:15		43
15/6	12:35		42
21/6	11:55	30.3	42.5
29/6	10:00	28.5	43
3/7	12:15	29.8	41.5
6/7	11:30	32	42
10/7	12:05	32.6	42
13/7	11:20	31.8	42
1/8	11:15		43
4/8	11:00	30.1	43
7/8	11:35	31.6	42.5
10/8	11:35	32	43
15/8	13:30	33.4	42.5
18/8	12:00	33.1	44
22/8	11:45	33.5	43
25/8	12:30	33.6	43
28/8	11:45	32.8	44
31/8	11:35	32.2	42
4/9	11:45	32.1	43
7/9	11:40	32.8	44
11/9	13:30	33.7	44
14/9	12:00	33.5	44
18/9	11:35	33.2	43
25/9	12:05	33.5	43
28/9	11:35	32.6	43
2/10	11:40	31.7	44
5/10	11:15	30.1	44
8/10	12:15	31.8	43
15/10	12:00	31.3	42
19/10	10:00	28.5	42
23/10	12:00	28.9	43
26/10	11:45	28.1	43
30/10	11:45	28.6	42

Date	Time	Temp.	Salin.
2/11	11:45	29.2	42
5/11	12:00	28.4	42
8/11	11:45	27.5	42
11/11	11:50	22.8	43
16/11	12:45	25.4	42
20/11	11:15	24.1	43
23/11	11:45	25.2	42
27/11	11:15	21.8	42
30/11	11:30	23.5	42
6/12	11:00	17	43
8/12	15:00	13.4	
10/12	11:30	14.5	44
13/12	11:45	16.1	44
18/12	10:30	19.2	43
21/12	11:00	19	43
5/1	11:35	17.3	
8/1	12:15	17.6	44
10/1	13:00	19.3	43
15/1	11:15	16	43
18/1	11:30	17.8	43
22/1	11:00	15.5	44
25/1	12:15	15.1	45
28/1	13:30	15.9	44
1/2	11:45	17.4	44
5/2	11:30	19	44
12/2	11:15	15.7	44
15/2	12:00	17.7	43
18/2	11:15	18	44
22/2	12:10	18.4	43
26/2	12:15	18.5	42
8/3	11:45	21	42
12/3	12:15	21.5	42
15/3	11:00	19.8	43
20/3	11:30	21.7	42
23/3	12:15	21.4	43
29/3	11:15	19.4	42.5
1/4	11:15	21.9	
6/4	11:00	20.1	42
9/4	12:00	21.8	42
13/4	12:15	22.9	42

Appendix 1.2 Jana

Raw data for the abiotic conditions recorded throughout the study period, where; (a) shallow site, (b) deep site.

(a)

Date	Time	Temp.	Salin.
9/6	11:55	30.6	40
24/6	11:50	29.8	40
29/7	11:30		40
12/8	12:45	31.2	40.5
27/8	12:00	32.4	40
10/9	11:30	32.2	40
21/10	13:05	30.6	41
15/11	12:15	28.3	41
15/12	12:40	23.6	42
29/1	12:10	19.3	42
19/2	11:10	18.9	42
15/4	12:15	20.7	41

(b)

Date	Time	Temp.	Salin.
27/5	13:20	27.5	41
9/6	14:35		40
24/6	11:00	29.4	39
29/7	10:10		39
14/8	9:40	31	40
27/8	10:45	32.2	40
10/9	10:00	32	40
21/10	10:50	30.4	41
15/11	10:45	28.5	41
15/12	10/45	23.4	42
29/1	10:30	19.1	42
19/2	9:55	18.7	42
15/4	9:50	20.5	41

Appendix 2

Algal Communities

Appendix 2.1 Jana (shallow)

2.1.1 Raw data of the algal community growing on **natural substrate** at Jana (shallow) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
5/94	Microalgae	4	0	0	0	0					
	Bryopsis	20	0	0	0	0					
	Feld./Hinck.	8	0	0	0	0					
	Sphacelaria	20	4	0	0	0					
	Gelidium	8	0	0	0	0					
	?Ulvella	16	0	0	0	0					
15/4/95	*Feld./Hinck.*	8	12	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	20	8	0	0	0
	Gelidium	0	8	0	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Centroceras	4	8	0	0	0	0	0	0	0	0
	Herposiphonia	0	0	0	0	0	12	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	12	0	0	0	0	24	0	0	0	0

2.1.2 Raw data of the algal community growing on the settlement plates in **Treatment 1** at Jana (shallow) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	*Cladophora*	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	12	0	0	0	16	4	0	0	0
	Sphacelaria	12	4	0	0	0	12	0	0	0	0
	Acrochaetium	0	8	0	0	0	8	8	0	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	?Ulvella	16	0	0	0	0	16	0	0	0	0
	?Peyssonnelia	4	0	0	0	0	0	0	0	0	0

2.1.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
24/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	16	16	0	0	0	28	4	0	0	0
	Sphacelaria	20	0	0	0	0	8	0	0	0	0
	Anotrichium	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	12	0	0	0	0	8	0	0	0	0
	?Ulvella	12	0	0	0	0	16	0	0	0	0
29/7/94	Microalgae	44	4	0	0	0	32	0	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	12	0	0	0	0
	Sphacelaria	16	4	0	0	0	8	0	0	0	0
	Herposiphonia	0	0	0	0	0	12	0	0	0	0
	?Ulvella	20	0	0	0	0	16	0	0	0	0
12/8/94	Microalgae	80	20	0	0	0	40	0	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	12	0	0	0	0
	?Ulvella	0	0	0	0	0	20	0	0	0	0
27/8/94	Microalgae	24	8	0	0	0	36	0	0	0	0
	Polysiphonia	0	8	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	?Ulvella	32	0	0	0	0	24	0	0	0	0
10/9/94	Microalgae	8	0	0	0	0	20	4	0	0	0
	Feld./Hinck.	8	4	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	8	0	0	0	0	0	0	0	0	0
	?Ulvella	32	0	0	0	0	24	0	0	0	0
21/10/94	Microalgae	36	0	0	0	0	48	0	0	0	0
	Acrochaetium	12	0	0	0	0	0	0	0	0	0
	?Ulvella	16	0	0	0	0	12	0	0	0	0
15/11/94	Microalgae	40	0	0	0	0	44	0	0	0	0
	Acrochaetium	12	0	0	0	0	4	0	0	0	0
	Ceramium	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	8	0	0	0	0	12	0	0	0	0
15/12/94	Microalgae						8	0	0	0	0
	Feld./Hinck.						4	4	0	0	0
	Ceramium						4	0	0	0	0
	?Ulvella						32	0	0	0	0
29/1/95	Microalgae						4	0	0	0	0
	Cladophora						0	4	0	0	0
	Feld./Hinck.						4	0	0	0	0
	Feld./Hinck.						4	0	0	0	0
	?Ulvella						28	0	0	0	0
19/2/95	*Feld./Hinck.*						4	20	8	0	0
	?Ulvella						12	0	0	0	0
15/4/95	*Feld./Hinck.*						8	0	0	0	0
	Sphacelaria						0	8	0	0	0
	?Ulvella						28	0	0	0	0

2.1.3 Raw data of the algal community growing on the settlement plates in **Treatment 2** at Jana (shallow) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	*Feld./Hinck.*	24	12	0	0	0	8	12	0	0	0
	Sphacelaria	8	0	0	0	0	12	0	0	0	0
	Acrochaetium	4	0	0	0	0	8	0	0	0	0
	Fosiella	4	0	0	0	0	8	0	0	0	0
	Ceramium	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	16	0	0	0	0
24/6/94	Microalgae	0	4	0	0	0	16	8	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	4	4	0	0	8	4	0	0	0
	Sphacelaria	0	4	0	0	0	0	4	0	0	0
	Anotrichium	4	4	0	0	0	8	0	0	0	0
	Ceramium	0	0	0	0	0	0	4	0	0	0
	Herposiphonia	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	24	28	4	0	0	4	8	4	0	0
	?Ulvella	8	0	0	0	0	4	0	0	0	0
29/7/94	Microalgae	0	12	8	0	0	0	28	0	0	0
	Sphacelaria	0	0	0	0	0	0	0	8	0	0
	Aglaothamnion	0	0	0	0	0	0	4	4	0	0
	Anotrichium	0	0	0	0	0	0	8	4	0	0
	Polysiphonia	4	48	28	0	0	0	0	24	20	0
12/8/94	Microalgae	0	0	0	0	0	0	48	16	0	0
	Sphacelaria	0	0	0	0	0	12	12	0	0	0
	Hypnea	0	0	0	0	16	0	0	0	0	0
	Polysiphonia	0	0	0	0	84	0	0	4	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
27/8/94	*Ceramium*	0	0	0	0	0	0	0	0	0	28
	Polysiphonia	0	0	0	0	96	0	0	0	0	60
10/9/94	Microalgae	0	16	24	8	8	0	0	0	0	0
	Hypnea	0	0	0	0	0	0	0	0	0	24
	Ceramium	0	0	0	0	8	0	0	0	0	0
	Polysiphonia	0	0	0	4	40	0	4	0	4	56
	?Ulvella	0	0	0	0	0	4	0	0	0	0
21/10/94	Microalgae	8	0	0	0	0					
	Chaetomorpha	0	4	0	0	0					
	Sphacelaria	4	20	0	0	0					
	Lobophora	0	8	0	0	0					
	Hypnea	4	8	12	0	0					
	Polysiphonia	4	0	0	0	0					
	?Ulvella	8	0	0	0	0					

2.1.3 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
15/11/94	*Cladophora*	0	4	0	0	0					
	Feld./Hinck.	0	8	0	0	0					
	Sphacelaria	16	8	0	0	0					
	Lobophora	4	12	0	0	0					
	Gelidium	0	4	0	0	0					
	Hypnea	0	12	0	0	0					
	Herposiphonia	4	0	0	0	0					
	?Ulvella	4	0	0	0	0					
15/12/94	*Cladophora*	0	4	0	0	0					
	Sphacelaria	16	16	0	0	0					
	Lobophora	0	4	12	0	0					
	Acrochaetium	0	4	0	0	0					
	Hypnea	0	8	4	0	0					
	Anotrichium	4	8	0	0	0					
	Herposphonia	4	4	0	0	0					
29/1/95	*Sphacelaria*	8	16	4	0	0					
	Lobophora	8	4	4	0	0					
	Hypnea	0	12	20	4	4					
19/2/95	*Hypnea*	0	0	0	0	100					
15/4/95	*Hypnea*	0	0	0	0	100					

2.1.4 Raw data of the algal community growing on the settlement plates in **Treatment 3** at Jana (shallow) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	*Feld./Hinck.*	8	8	0	0	0	4	0	0	0	0
	Sphacelaria	16	4	0	0	0	12	0	0	0	0
	Acrochaetium	8	0	0	0	0	8	0	0	0	0
	Fosiella	8	0	0	0	0	16	0	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	Herposiphonia	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	4	0	0	0	0	8	0	0	0	0
	?Ulvella	16	0	0	0	0	12	0	0	0	0

2.1.4 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
24/6/94	Microalgae	16	0	0	0	0	0	0	0	0	0
	Enteromorpha	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	20	0	0	0	0
	Sphacelaria	4	0	0	0	0	16	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Centroceras	4	0	0	0	0	0	0	0	0	0
	Ceramium	4	4	0	0	0	0	0	0	0	0
	Herposiphonia	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	4	0	0	0	12	4	0	0	0
	?Ulvella	12	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	0	0	0	0	0	12	0	0	0	0
29/7/94	Microalgae	32	8	0	0	0	40	16	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	8	0	0	0	0	12	0	0	0	0
	Lobophora	12	0	0	0	0	0	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	16	0	0	0	0	12	0	0	0	0
12/8/94	Microalgae	0	64	4	0	0	0	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	8	0	0	0	0	32	4	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	?Ulvella	16	0	0	0	0	36	0	0	0	0
27/8/94	Microalgae	4	0	0	0	0	16	0	0	0	0
	Feld./Hinck.	8	28	0	0	0	12	0	0	0	0
	Sphacelaria	16	0	0	0	0	16	0	0	0	0
	Herposiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	4	0	0	0	0	4	0	0	0	0
10/9/94	Microalgae	24	0	0	0	0	8	0	0	0	0
	Feld./Hinck.	12	0	0	0	0	4	4	0	0	0
	Sphacelaria	12	0	0	0	0	16	0	0	0	0
	Acrochaetium	0	0	0	0	0	4	0	0	0	0
	?Ulvella	20	0	0	0	0	20	0	0	0	0
21/10/94	Microalgae						32	0	0	0	0
	Acrochaetium						4	0	0	0	0
	?Ulvella						36	0	0	0	0

2.1.5 Raw data of the algal community growing on the settlement plates in **Treatments 5 and 6** at Jana (shallow) throughout the study period.

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	*Bryopsis*	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	12	8	0	0	0	8	16	0	0	0
	Sphacelaria	8	0	0	0	0	8	0	0	0	0
	Acrochaetium	0	12	0	0	0	0	12	0	0	0
	Gelidium	4	0	0	0	0	0	0	0	0	0
	Fosiella	4	0	0	0	0	8	0	0	0	0
	Ceramium	4	0	0	0	0	4	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	20	0	0	0	0
24/6/94	*Feld./Hinck.*	20	16	0	0	0	24	12	0	0	0
	Sphacelaria	12	0	0	0	0	20	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	8	4	0	0	0	4	0	0	0	0
	?Ulvella	12	0	0	0	0	8	0	0	0	0
29/7/94	Microalgae	28	0	0	0	0	12	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	24	0	0	0	0
	Sphacelaria	0	0	0	0	0	20	0	0	0	0
	Anotrichium	8	0	0	0	0	0	0	0	0	0
	Herposiphonia	8	0	0	0	0	0	0	0	0	0
	Polysiphonia	20	0	0	0	0	0	0	0	0	0
	?Ulvella	8	0	0	0	0	24	0	0	0	0
12/8/94	Microalgae	28	4	0	0	0	12	80	4	0	0
	Feld./Hinck.	12	8	4	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	8	0	0	0	0	4	0	0	0	0
27/8/94	Microalgae	28	0	0	0	0	20	64	0	0	0
	Feld./Hinck.	16	0	0	0	0	0	0	0	0	0
	Acrochaetium	8	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	4	0	0	0	0	0	0	0	0	0
10/9/94	Microalgae	20	0	0	0	0	16	0	0	0	0
	Feld./Hinck.	12	0	0	0	0	8	0	0	0	0
	Sphacelaria	0	0	0	0	0	12	0	0	0	0
	Acrochaetium	8	4	0	0	0	0	0	0	0	0
	?Ulvella	16	0	0	0	0	24	0	0	0	0

2.1.5 (contd.)

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
21/10/94	Microalgae	20	4	0	0	0	12	0	0	0	0
	Enteromorpha	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	4	0	0	0	4	0	0	0	0
	Acrochaetium	12	12	0	0	0	4	0	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	0	0	0	0	0
15/11/94	Microalgae	16	0	0	0	0	24	8	0	0	0
	Enteromorpha	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	20	0	0	0	4	0	0	0	0
	Acrochaetium	24	0	0	0	0	0	0	0	0	0
	Herposiphonia	8	12	0	0	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	0	0	0	0	0
15/12/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	32	0	0	0	8	8	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	12	0	0	0	0	0	0	0	0	0
	Herposiphonia	16	8	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	52	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	0	0	0	0	0

Appendix 2.2 Jana (deep)

2.2.1 Raw data of the algal community growing on **natural substrate** at Jana (deep) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
5/94	Microalgae	0	4	0	0	0					
	Bryopsis	20	0	0	0	0					
	Feld./Hinck.	8	0	0	0	0					
	Sphacelaria	8	0	0	0	0					
	Gelidium	4	0	0	0	0					
	Polysiphonia	12	0	0	0	0					
	?Ulvella	8	0	0	0	0					
	?Peyssonnelia	20	0	0	0	0					
15/4/95	Microalgae	8	0	0	0	0	16	4	4	0	0
	Cladophora	0	4	0	0	0	0	4	0	0	0
	Bryopsis	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	4	0	0	0	0
	Acrochaetium	8	0	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Polysiphonia	8	4	0	0	0	0	4	0	0	0
	?Ulvella	12	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	4	0	0	0	0	20	0	0	0	0

2.2.2 Raw data of the algal community growing on the settlement plates in **Treatment 1** at Jana (deep) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/5/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Bryopsis	0	0	0	0	0	4	12	0	0	0
	Feld./Hinck.	0	24	0	0	0	0	16	0	0	0
	Sphacelaria	4	0	0	0	0	4	0	0	0	0
	Acrochaetium	0	4	0	0	0	0	0	0	0	0
	?Ulvella	24	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	28	0	0	0	0

2.2.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	12	0	0	0	0
	Feld./Hinck.	4	4	0	0	0	0	0	0	0	0
	Sphacelaria	0	4	0	0	0	0	0	0	0	0
	Acrochaetium	8	12	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	4	0	0	0	0	0	0	0	0
	?Ulvella	20	0	0	0	0	16	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	32	0	0	0	0
24/6/94	Microalgae	0	0	0	0	0	20	0	0	0	0
	Feld./Hinck.	12	0	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	8	0	0	0	0	4	0	0	0	0
	?Ulvella	32	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	36	0	0	0	0	48	0	0	0	0
29/7/94	Microalgae	4	0	0	0	0	24	0	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Bryopsis	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	8	0	0	0	0
	Sphacelaria	4	4	0	0	0	4	0	0	0	0
	Acrochaetium	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	24	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	36	0	0	0	0	32	0	0	0	0
14/8/94	Microalgae	4	0	0	0	0	12	0	0	0	0
	Feld./Hinck.	24	0	0	0	0	0	0	0	0	0
	Sphacelaria	0	0	0	0	0	4	0	0	0	0
	Fosiella	8	0	0	0	0	4	0	0	0	0
	Anotrichium	0	0	0	0	0	12	0	0	0	0
	?Ulvella	28	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	28	0	0	0	0
27/8/94	Microalgae	12	0	0	0	0	12	4	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	12	0	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	0	0	0	0	0	12	0	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	?Ulvella	24	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	32	0	0	0	0
10/9/94	Microalgae	4	4	0	0	0	28	4	0	0	0
	Sphacelaria	8	0	0	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	8	0	0	0	0	0	0	0	0	0
	?Ulvella	20	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	12	0	0	0	0

2.2.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
21/10/94	Microalgae	40	0	0	0	0	28	8	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	0	0	0	0	0	0	4	0	0	0
	?Ulvella	16	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	28	0	0	0	0
15/11/94	Microalgae	4	0	0	0	0	16	0	0	0	0
	Feld./Hinck.	8	4	0	0	0	0	0	0	0	0
	Acrochaetium	0	4	0	0	0	4	0	0	0	0
	Aglaothamnion	0	0	0	0	0	4	0	0	0	0
	?Ulvella	20	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	40	0	0	0	0	48	0	0	0	0
15/12/94	Microalgae	8	0	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	4	4	0	0	0
	Acrochaetium	0	0	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	8	0	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	Ceramium	0	4	0	0	0	0	0	0	0	0
	?Ulvella	28	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	28	0	0	0	0	40	0	0	0	0
29/1/95	*Cladophora*	0	4	0	0	0	4	4	0	0	0
	Bryopsis	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	8	0	0	0	0	0	0	0	0	0
	Aglaothamnion	4	0	0	0	0	0	0	0	0	0
	Anotrichium	0	0	0	0	0	12	0	0	0	0
	Polysiphonia	0	4	0	0	0	0	4	0	0	0
	?Ulvella	16	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	24	0	0	0	0
19/2/95	Microalgae	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	4	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	4	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Anotrichium	0	0	0	0	0	16	4	0	0	0
	Ceramium	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	0	0	0	0	0	4	0	0	0
	?Ulvella	20	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	28	0	0	0	0
15/4/95	Microalgae	0	0	0	0	0	12	0	0	0	0
	Sphacelaria	4	0	0	0	0	4	0	0	0	0
	Acrochaetium	0	4	0	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	8	0	0	0	0
	Polysiphonia	4	8	0	0	0	0	0	0	0	0
	?Ulvella	28	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	40	0	0	0	0

2.2.3 Raw data of the algal community growing on the settlement plates in **Treatment 2** at Jana (deep) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/5/94	Microalgae	8	4	0	0	0	8	0	0	0	0
	Bryopsis	0	4	0	0	0	4	4	0	0	0
	Feld./Hinck.	4	16	0	0	0	4	8	8	0	0
	Sphacelaria	0	8	0	0	0	4	4	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Anotrichium	0	0	0	0	0	4	4	0	0	0
	Polysiphonia	4	0	0	0	0	0	4	0	0	0
	?Ulvella	16	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	12	0	0	0	0
9/6/94	Microalgae	0	0	0	0	0	4	4	0	0	0
	Bryopsis	0	0	0	0	0	4	4	0	0	0
	Feld./Hinck.	0	8	4	0	0	4	8	0	0	0
	Sphacelaria	4	4	0	0	0	0	0	0	0	0
	Acrochaetium	16	4	4	0	0	8	4	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	0	0	0	0	0	16	8	0	0
	?Ulvella	8	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	28	0	0	0	0
24/6/94	Microalgae	12	0	0	0	0	8	4	0	0	0
	Feld./Hinck.	4	16	0	0	0	0	0	0	0	0
	Sphacelaria	8	8	0	0	0	0	0	0	0	0
	Acrochaetium	0	4	0	0	0	4	0	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	0	0	0	0	36	16	0	0	0
	?Ulvella	8	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	0	0	0	0	0	12	0	0	0	0
29/7/94	Microalgae	24	0	0	0	0	0	0	0	0	0
	Cladophora	0	8	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	12	8	0	0	0
	Sphacelaria	4	0	0	0	0	8	0	0	0	0
	Acrochaetium	0	20	0	0	0	4	8	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	16	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	24	0	0	0	0
12/8/94	Microalgae	0	0	0	0	0	12	4	0	0	0
	Feld./Hinck.	8	0	0	0	0	0	4	0	0	0
	Sphacelaria	12	0	0	0	0	4	4	0	0	0
	Acrochaetium	12	0	0	0	0	8	36	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	?Ulvella	24	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	32	0	0	0	0	16	0	0	0	0

2.2.3 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/8/94	Microalgae	4	12	0	0	0	12	4	0	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	4	0	0	0
	Sphacelaria	12	8	0	0	0	8	16	0	0	0
	Acrochaetium	4	8	0	0	0	4	20	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	16	0	0	0	0
10/9/94	Microalgae	4	16	0	0	0	0	16	4	0	0
	Bryopsis	0	8	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	8	0	0	0	0	0	0	0	0
	Sphacelaria	0	8	0	0	0	0	8	0	0	0
	Acrochaetium	0	12	0	0	0	0	20	24	0	0
	Ceramium	0	0	4	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	28	0	0	0	0	20	0	0	0	0
21/10/94	Microalgae	4	16	0	0	0	4	12	0	0	0
	Cladophora	0	4	0	0	0	0	0	4	0	0
	Sphacelaria	0	12	0	0	0	0	16	4	0	0
	Acrochaetium	0	48	0	0	0	0	36	4	0	0
	?Ulvella	8	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	16	0	0	0	0
15/11/94	Microalgae	4	4	0	0	0	0	0	0	0	0
	Bryopsis	4	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	4	0	0	0	0	4	0	0	0	0
	Sphacelaria	0	16	0	0	0	8	16	0	0	0
	Lobophora	0	0	0	0	0	4	16	0	0	0
	Acrochaetium	32	8	0	0	0	20	16	0	0	0
	Aglaothamnion	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	0	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	8	0	0	0	0
15/12/94	*Cladophora*	0	4	0	0	0					
	Sphacelaria	8	4	0	0	0					
	Acrochaetium	28	16	0	0	0					
	?Ulvella	4	0	0	0	0					
	?Peyssonnelia	28	0	0	0	0					
29/1/95	*Cladophora*	4	4	0	0	0	4	4	0	0	0
	Trichosolen	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	0	0	0	0	0	0	16	0	0	0
	Acrochaetium	0	0	0	0	0	24	12	0	0	0
	Aglaothamnion	0	12	8	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Crouania	0	0	8	0	0	0	0	0	0	0
	?Peyssonnelia	0	0	0	0	0	12	0	0	0	0

2.2.3 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
19/2/95	*Cladophora*	0	8	8	0	0	0	4	8	0	0
	Bryopsis	0	8	4	0	0	0	0	0	0	0
	Feld./Hinck.	0	0	12	0	0	0	0	0	0	0
	Sphacelaria	0	8	0	0	0	0	20	4	0	0
	Acrochaetium	4	4	0	0	0	16	0	0	0	0
	Hypnea	0	0	0	0	0	0	0	0	4	16
	Aglaothamnion	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	0	12	4	0	0	0	4	0	0	0
	?Peyssonnelia	12	0	0	0	0	8	0	0	0	0
15/4/95	Microalgae	4	0	0	0	0	8	0	0	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	8	4	0	0	0	8	0	0	0	0
	Lobophora	0	0	0	0	0	20	0	0	0	0
	Acrochaetium	16	12	0	0	0	12	4	0	0	0
	Hypnea	0	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	0	0	0	0	12	0	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	28	0	0	0	0	16	0	0	0	0

2.2.4 Raw data of the algal community growing on the settlement plates in **Treatment 3** at Jana (deep) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/5/94	Microalgae	4	16	0	0	0	0	0	0	0	0
	Bryopsis	8	8	0	0	0	0	12	0	0	0
	Feld./Hinck.	12	12	0	0	0	8	4	0	0	0
	Sphacelaria	0	0	0	0	0	0	4	0	0	0
	Fosiella	0	0	0	0	0	12	0	0	0	0
	Anotrichium	0	0	0	0	0	0	8	0	0	0
	Centroceras	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	0	0	0	0	0	0	4	0	0	0
	?Ulvella	8	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	12	0	0	0	0

2.2.4 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
9/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Bryopsis	4	4	0	0	0	0	4	0	0	0
	Feld./Hinck.	4	4	0	0	0	0	4	0	0	0
	Sphacelaria	0	0	0	0	0	20	0	0	0	0
	Acrochaetium	0	4	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	8	0	0	0	0
	Polysiphonia	0	4	0	0	0	0	0	0	0	0
	?Ulvella	20	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	16	0	0	0	0
24/6/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Enteromorpha	0	0	0	0	0	4	0	0	0	0
	Cladophora	4	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	4	8	0	0	0
	Sphacelaria	4	0	0	0	0	8	0	0	0	0
	Acrochaetium	0	0	0	0	0	0	4	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Aglaothamnion	0	0	0	0	0	0	4	0	0	0
	Anotrichium	8	0	0	0	0	8	0	0	0	0
	Polysiphonia	24	4	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	20	0	0	0	0
29/7/94	Microalgae	8	0	0	0	0	8	4	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	16	4	0	0	0	8	0	0	0	0
	Sphacelaria	8	0	0	0	0	4	4	0	0	0
	Acrochaetium	8	4	0	0	0	16	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	20	0	0	0	0
12/8/94	Microalgae	12	0	0	0	0	20	4	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	8	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	?Ulvella	24	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	40	0	0	0	0
27/8	Microalgae	4	0	0	0	0	32	0	0	0	0
	Feld./Hinck.	12	8	0	0	0	12	0	0	0	0
	Sphacelaria	8	0	0	0	0	0	0	0	0	0
	Acrochaetium	8	0	0	0	0	12	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	8	0	0	0	0	0	0	0	0
	?Ulvella	8	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	8	0	0	0	0

2.2.4 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
10/9/94	Microalgae	20	0	0	0	0	16	0	0	0	0
	Cladophora	0	4	0	0	0	0	4	0	0	0
	Feld./Hinck.	8	0	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	12	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	16	0	0	0	0
21/10/94	Microalgae	20	4	0	0	0	20	4	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	0	4	0	0	0	0	0	0	0	0
	Acrochaetium	0	4	0	0	0	12	4	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	?Ulvella	16	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	24	0	0	0	0
15/11/94	Microalgae	12	0	0	0	0	16	0	0	0	0
	Acrochaetium	8	0	0	0	0	8	0	0	0	0
	?Ulvella	16	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	36	0	0	0	0	56	0	0	0	0
15/12/94	Microalgae	4	4	0	0	0	16	0	0	0	0
	Cladphora	4	0	0	0	0	0	0	0	0	0
	Bryopsis	8	0	0	0	0	8	0	0	0	0
	Feld./Hinck.	4	4	0	0	0	4	0	0	0	0
	Sphacelaria	0	4	0	0	0	0	0	0	0	0
	Acrochaetium	0	0	0	0	0	12	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	16	0	0	0	0
29/1/95	Microalgae	12	8	0	0	0	16	4	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	0	4	0	0	0	0	0	0	0	0
	Aglaothamnion	0	4	0	0	0	0	0	0	0	0
	Anotrichium	8	0	0	0	0	0	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	4	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	24	0	0	0	0

2.2.4 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
19/2/95	Microalgae	0	4	0	0	0	0	0	0	0	0
	Bryopsis	0	4	0	0	0	0	20	0	0	0
	Feld./Hinck.	0	16	0	0	0	0	0	0	0	0
	Polysiphonia	0	12	0	0	0	4	0	0	0	0
	?Ulvella	12	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	24	0	0	0	0	48	0	0	0	0
15/4/95	*Sphacelaria*	8	0	0	0	0					
	Acrochaetium	4	0	0	0	0					
	Fosiella	8	0	0	0	0					
	Polysiphonia	8	16	0	0	0					
	?Ulvella	16	0	0	0	0					
	?Peyssonnelia	16	0	0	0	0					

2.2.5 Raw data of the algal community growing on the settlement plates in **Treatment 4** at Jana (deep) throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/5/94	Microalgae	8	0	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	4	12	0	0	0
	Feld./Hinck.	0	20	0	0	0	0	12	0	0	0
	Sphacelaria	0	8	0	0	0	4	4	0	0	0
	Fosiella	4	0	0	0	0	12	0	0	0	0
	Centroceras	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	0	0	0	0	0	4	0	0	0
	?Ulvella	24	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	4	0	0	0	0
9/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Bryopsis	0	8	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	4	0	0	0	4	0	0	0	0
	Sphacelaria	0	0	0	0	0	4	0	0	0	0
	Acrochaetium	0	0	0	0	0	8	0	0	0	0
	Fosiella	4	0	0	0	0	12	0	0	0	0
	Polysiphonia	0	0	0	0	0	8	4	0	0	0
	?Ulvella	16	0	0	0	0	16	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	4	0	0	0	0

2.2.5 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
24/6/94	Microalgae	0	0	0	0	0	8	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	12	4	0	0	0
	Sphacelaria	0	0	0	0	0	4	0	0	0	0
	Acrochaetium	0	0	0	0	0	8	0	0	0	0
	Fosiella	12	0	0	0	0	8	0	0	0	0
	Anotrichium	12	0	0	0	0	0	0	0	0	0
	Polysiphonia	12	4	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	8	0	0	0	0
29/7/94	Microalgae	36	0	0	0	0	24	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	8	0	0	0	0
	Acrochaetium	0	0	0	0	0	4	8	0	0	0
	Anotrichium	16	0	0	0	0	12	0	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	8	0	0	0	0	4	12	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	8	0	0	0	0
14/8/94	Microalgae	16	4	0	0	0	16	8	0	0	0
	Feld./Hinck.	8	4	0	0	0	16	4	0	0	0
	Sphacelaria	8	0	0	0	0	8	0	0	0	0
	Acrochaetium	0	0	0	0	0	0	4	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Anotrichium	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	20	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	12	0	0	0	0	0	0	0	0	0
27/8	Microalgae	20	20	0	0	0	16	4	0	0	0
	Feld./Hinck.	0	0	0	0	0	8	12	0	0	0
	Acrochaetium	0	4	0	0	0	12	16	0	0	0
	Anotrichium	8	0	0	0	0	0	0	0	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	8	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	8	0	0	0	0
10/9/94	Microalgae	12	28	0	0	0	8	0	0	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	8	4	0	0	0
	Sphacelaria	4	0	0	0	0	0	4	0	0	0
	Acrochaetium	4	4	0	0	0	4	4	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	Herposiphonia	4	4	0	0	0	0	0	0	0	0
	Polysiphonia	8	0	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	16	0	0	0	0

2.2.5 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
21/10/94	Microalgae	28	8	0	0	0	20	8	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	0	0	0	0	0	0	4	0	0	0
	Acrochaetium	4	12	0	0	0	16	8	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	4	0	0	0	0
	?Peyssonnelia	32	0	0	0	0	20	0	0	0	0
15/11/94	Microalgae	8	4	0	0	0	8	0	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Bryopsis	16	4	0	0	0	12	0	0	0	0
	Acrochaetium	4	0	0	0	0	12	0	0	0	0
	Anotrichium	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	12	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	16	0	0	0	0
15/12/94	*Bryopsis*	12	0	0	0	0	12	8	0	0	0
	Acrochaetium	4	0	0	0	0	8	0	0	0	0
	Fosiella	16	0	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	12	0	0	0	0
29/1/95	Microalgae	0	0	0	0	0	8	0	0	0	0
	Bryopsis	0	0	0	0	0	12	0	0	0	0
	Sphacelaria	4	4	0	0	0	0	0	0	0	0
	Acrochaetium	12	0	0	0	0	0	0	0	0	0
	Aglaothamnion	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	4	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	0	0	0	0	0	4	0	0	0	0
19/2/95	Microalgae	0	0	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Bryopsis	0	8	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	0	0	0	0	0	0	8	0	0	0
	Aglaothamnion	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	0	4	0	0	0	4	12	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
	?Peyssonnelia	20	0	0	0	0	0	0	0	0	0
15/4/95	*Acrochaetium*	0	0	0	0	0	4	0	0	0	0
	Ceramium	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	0	0	0	0	20	8	0	0	0
	?Ulvella	12	0	0	0	0	4	0	0	0	0

2.2.6 Raw data of the algal community growing on the settlement plates in **Treatments 5 and 6** at Jana (deep) throughout the study period.

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/5/94	Microalgae	8	0	0	0	0	4	0	0	0	0
	Chaetomorpha	0	0	0	0	0	0	4	0	0	0
	Bryopsis	0	8	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	20	0	0	0	4	8	0	0	0
	Sphacelaria	4	8	0	0	0	0	4	0	0	0
	Fosiella	0	0	0	0	0	12	0	0	0	0
	Centroceras	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	0	0	0	0	0	4	0	0	0	0
	?Ulvella	16	0	0	0	0	8	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	24	0	0	0	0
9/6/94	Microalgae	0	0	0	0	0	8	0	0	0	0
	Feld./Hinck.	12	8	0	0	0	8	0	0	0	0
	Sphacelaria	4	0	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Anotrichium	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	4	0	0	0	0	0	0	0	0	0
	?Ulvella	16	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	32	0	0	0	0	24	0	0	0	0
24/6/94	Microalgae	4	0	0	0	0	12	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	0	0	0	0	0	4	4	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Aglaothamnion	0	0	0	0	0	0	4	0	0	0
	Anotrichium	4	0	0	0	0	4	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	16	0	0	0	0	0	0	0	0	0
	?Ulvella	12	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	32	0	0	0	0	32	0	0	0	0
29/7/94	Microalgae	8	0	0	0	0	20	0	0	0	0
	Feld./Hinck.	12	8	0	0	0	4	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	8	0	0	0	0	4	0	0	0	0
	?Ulvella	16	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	28	0	0	0	0	32	0	0	0	0
12/8/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	12	8	0	0	0
	Sphacelaria	0	0	0	0	0	8	4	0	0	0
	Acrochaetium	8	4	0	0	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	?Ulvella	28	0	0	0	0	24	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	20	0	0	0	0

2.2.6 (contd.)

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/8/94	Microalgae	40	12	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	4	0	0	0
	Sphacelaria	0	4	0	0	0	12	0	0	0	0
	Acrochaetium	8	0	0	0	0	4	4	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	?Ulvella	12	0	0	0	0	20	0	0	0	0
	?Peyssonnelia	8	0	0	0	0	24	0	0	0	0
10/9/94	Microalgae	28	20	0	0	0	24	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	0	0	0	0	0
	Sphacelaria	0	0	0	0	0	4	0	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	?Ulvella	16	0	0	0	0	28	0	0	0	0
	?Peyssonnelia	0	0	0	0	0	20	0	0	0	0
21/10/94	Microalgae	40	0	0	0	0	24	12	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Acrochaetium	12	0	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	12	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	20	0	0	0	0
15/11/94	Microalgae	24	0	0	0	0	16	0	0	0	0
	Bryopsis	4	0	0	0	0	0	0	0	0	0
	Acrochaetium	4	0	0	0	0	4	0	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	?Ulvella	8	0	0	0	0	32	0	0	0	0
	?Peyssonnelia	16	0	0	0	0	24	0	0	0	0
15/12/94	Microalgae	16	8	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	?Ulvella	20	0	0	0	0	32	0	0	0	0
	?Peyssonnelia	32	0	0	0	0	24	0	0	0	0
29/1/95	Microalgae	8	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	8	0	0	0	4	4	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	16	0	0	0	0
	?Ulvella	4	0	0	0	0	40	0	0	0	0
	?Peyssonnelia	44	0	0	0	0	20	0	0	0	0
19/2/95	Microalgae	8	0	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Bryopsis	0	4	4	0	0	0	0	0	0	0
	Feld./Hinck.	0	12	0	0	0	0	0	0	0	0
	Sphacelaria	0	0	0	0	0	0	8	0	0	0
	Acrochaetium	4	0	0	0	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	?Ulvella	8	0	0	0	0	28	0	0	0	0
	?Peyssonnelia	48	0	0	0	0	32	0	0	0	0
15/4/95	Microalgae	0	0	0	0	0	8	0	0	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	12	0	0	0	0	0	4	0	0	0
	Sphacelaria	8	4	0	0	0	4	0	0	0	0
	Polysiphonia	0	4	0	0	0	0	4	0	0	0
	?Ulvella	12	0	0	0	0	16	0	0	0	0
	?Peyssonnelia	28	0	0	0	0	40	0	0	0	0

Appendix 2.3 Abu Ali

2.3.1 Raw data of the algal community growing on **natural substrate** at Abu Ali throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
5/94	*Sphacelaria*	4	24	12	0	0					
	Dictyota	0	8	0	0	0					
	Padina	0	4	0	0	0					
	Jania	0	0	4	0	0					
	Centroceras	4	0	0	0	0					
	Ceramium	0	4	0	0	0					
	Polysiphonia	8	28	0	0	0					
13/4/95	*Chaetomorpha*	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	0	8	8	0	0	0	16	8	0	0
	Dictyota	0	0	0	0	0	0	0	8	0	0
	Padina	0	0	0	8	12	0	0	8	0	8
	Phaeophyte (juv)	0	4	0	0	0	0	0	4	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Jania	0	0	4	0	0	0	0	0	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	28	0	0	0	8	8	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0

2.3.2 Raw data of the algal community growing on the settlement plates in **Treatment 1** at Abu Ali throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
1/6/94	*Enteromorpha*	0	4	0	0	0	0	0	4	0	0
	Chaetomorpha	0	0	4	0	0	0	0	0	8	0
	Bryopsis	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	8	0	0	0
	Sphacelaria	4	8	4	0	0	0	44	0	0	0
	Padina	0	0	0	4	0	0	0	0	4	0
	Gelidium	0	8	0	0	0	0	0	0	0	0
	Centroceras	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	4	20	16	0	0	0	12	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	4	0	0

2.3.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
7/6/94	*Chaetomorpha*	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	4	0	0	0	0	8	0	0	0	0
	Sphacelaria	4	0	0	0	0	4	32	0	0	0
	Padina	0	0	0	4	12	0	0	0	0	0
	Centroceras	0	4	20	0	0	0	0	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	Crouania	0	4	0	0	0	0	0	0	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	20	20	0	0	4	8	0	0	0
12/6/94	*Chaetomorpha*	0	4	0	0	0	0	0	4	4	0
	Cladophora	0	4	0	0	0	0	4	0	0	0
	Feld./Hinck.	0	0	0	0	0	8	4	0	0	0
	Sphacelaria	8	20	0	0	0	16	32	0	0	0
	Padina	0	0	8	16	0	0	0	4	0	0
	Centroceras	0	8	0	0	0	0	0	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	0	0	0	0	4	8	0	0	0
15/6/94	*Enteromorpha*	0	4	0	0	0	0	0	0	0	0
	Chaetomorpha	0	0	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	12	0	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	8	16	0	0	0	36	12	0	0	0
	Padina	0	0	0	8	16	0	0	0	0	0
	Crouania	0	4	0	0	0	0	0	0	0	0
	Herposiphonia	12	0	0	0	0	0	0	0	0	0
	Polysiphonia	16	4	0	0	0	8	0	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
21/6/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Enteromorpha	8	4	0	0	0	8	16	0	0	0
	Chaetomorpha	0	0	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	12	0	0	0	0	0	0	0	0	0
	Sphacelaria	12	8	0	0	0	20	12	0	0	0
	Padina	0	0	4	0	0	0	0	0	0	0
	Ceramium	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	20	8	0	0	0	4	0	0	0	0
	?Ulvella	4	0	0	0	0	8	0	0	0	0
29/6/94	Microalgae	8	0	0	0	0	8	0	0	0	0
	Enteromorpha	0	4	0	0	0	0	0	0	0	0
	Bryopsis	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	8	0	0	0	0	4	0	0	0	0
	Sphacelaria	32	0	0	0	0	32	8	0	0	0
	Padina	0	0	0	0	0	0	0	8	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	4	12	0	0	0	12	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	4	0	0	0

2.3.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
3/7/94	Microalgae	12	0	0	0	0	8	0	0	0	0
	Enteromorpha	0	0	0	0	0	0	4	0	0	0
	Chaetomorpha	0	0	0	0	0	0	8	0	0	0
	Cladophora	0	0	4	0	0	0	16	4	0	0
	Bryopsis	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	24	16	0	0	0	8	0	0	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	8	0	0	0	12	4	0	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0
6/7/94	Microalgae	8	0	0	0	0	0	8	0	0	0
	Enteromorpha	0	0	4	0	0	0	0	0	0	0
	Chaetomorpha	0	0	0	0	0	0	8	4	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	12	12	0	0	0	28	4	0	0	0
	Padina	0	0	0	8	0	0	0	0	0	0
	Ceramium	4	0	0	0	0	0	0	0	0	0
	Herposiphonia	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	4	20	4	0	0	0	24	0	0	0
10/7/94	Microalgae	12	12	0	0	0	4	0	0	0	0
	Enteromorpha	0	8	0	0	0	0	0	0	0	0
	Chaetomorpha	0	0	0	0	0	0	0	4	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	28	8	0	0	0	20	20	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	8	0	0	0	0	20	12	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
13/7/94	Microalgae	8	12	0	0	0	8	0	0	0	0
	Enteromorpha	0	8	0	0	0	0	12	4	0	0
	Chaetomorpha	0	0	0	0	0	0	0	0	0	0
	Sphacelaria	8	20	0	0	0	4	4	0	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Polysiphonia	4	16	0	0	0	12	16	0	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0
27/7/94	Microalgae	4	20	0	0	0	8	24	0	0	0
	Chaetomorpha	0	4	0	0	0	0	4	4	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	20	0	0	0	0	8	0	0	0
	Centroceras	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	20	0	0	0	12	32	0	0	0
10/8/94	Microalgae	12	12	0	0	0	8	16	0	0	0
	Chaetomorpha	4	0	0	0	0	4	4	0	0	0
	Sphacelaria	12	12	0	0	0	4	4	0	0	0
	Herposiphonia	0	16	0	0	0	0	0	0	0	0
	Polysiphonia	8	8	0	0	0	4	20	0	0	0

2.3.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
28/8/94	Microalgae	4	40	0	0	0	4	40	4	0	0
	Sphacelaria	0	28	0	0	0	4	20	0	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	8	4	0	0	0	4	20	0	0	0
11/9/94	Microalgae	4	8	0	0	0	8	20	0	0	0
	Chaetomorpha	8	0	0	0	0	0	12	0	0	0
	Sphacelaria	12	16	0	0	0	20	8	0	0	0
	Polysiphonia	12	12	0	0	0	4	0	0	0	0
19/10/94	Microalgae	0	0	0	0	0	4	8	0	0	0
	Chaetomorpha	0	8	0	0	0	4	0	0	0	0
	Sphacelaria	4	32	0	0	0	12	0	0	0	0
	Fosiella	0	0	0	0	0	16	0	0	0	0
	Polysiphonia	12	20	0	0	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
16/11/94	*Enteromorpha*	0	4	0	0	0	0	0	0	0	0
	Chaetomorpha	0	8	0	0	0	0	0	0	0	0
	Sphacelaria	0	16	0	0	0	0	0	0	0	0
	Padina	0	4	0	0	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	40	0	0	0	0
	Ceramium	0	0	0	0	0	24	0	0	0	0
	Herposiphonia	4	0	0	0	0	4	0	0	0	0
	Polysiphonia	12	32	0	0	0	8	0	0	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
13/12/94	*Enteromorpha*	0	0	0	0	0	0	4	0	0	0
	Chaetomorpha	0	8	0	0	0	0	8	4	0	0
	Cladophora	0	0	0	0	0	0	12	0	0	0
	Sphacelaria	0	4	0	0	0	0	0	0	0	0
	Jania	4	0	4	0	0	0	0	0	0	0
	Hypnea	0	0	0	0	0	0	8	0	0	0
	Ceramium	0	4	4	0	0	0	4	0	0	0
	Spyridia	0	4	0	0	0	0	0	0	0	0
	Chondria	0	0	0	0	0	0	4	0	0	0
	Herposiphonia	0	4	0	0	0	4	12	0	0	0
	Polysiphonia	4	36	8	0	0	12	16	0	0	0
	Phaeophyte (juv)	0	8	4	0	0	0	0	0	0	0
28/1/95	*Enteromorpha*	0	4	0	0	0	0	0	0	0	0
	Chaetomorpha	0	4	0	0	0	0	0	0	0	0
	Cladophora	0	0	0	0	0	0	8	0	0	0
	Sphacelaria	8	20	8	0	0	4	20	0	0	0
	Fosiella	0	0	0	0	0	12	0	0	0	0
	Polysiphonia	12	20	0	0	0	20	24	0	0	0
	Phaeophyte (juv)	0	0	8	0	0	0	0	0	0	0
18/2/95	*Chaetomorpha*	0	4	0	0	0	0	0	0	0	0
	Cladophora	0	0	0	0	0	0	0	0	4	0
	Feld./Hinck.	0	0	0	0	0	0	0	0	4	4
	Sphacelaria	0	12	0	0	0	0	20	20	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Herposiphonia	4	8	0	0	0	0	12	0	0	0
	Polysiphonia	8	44	8	0	0	8	12	0	0	0

2.3.2 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
13/4/95	*Enteromorpha*	0	0	0	0	0	0	4	0	0	0
	Sphacelaria	8	16	8	0	0	4	12	20	0	0
	Fosiella	0	0	0	0	0	12	0	0	0	0
	Jania	0	0	0	0	0	0	0	4	0	0
	Hypnea	0	0	0	0	0	0	4	0	0	0
	Centroceras	0	0	0	0	0	0	0	4	0	0
	Herposiphonia	0	4	0	0	0	0	12	0	0	0
	Polysiphonia	8	20	4	0	0	0	4	0	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
	Phaeophyte (juv)	0	4	4	0	0	0	0	0	0	0

2.3.3 Raw data of the algal community growing on the settlement plates in **Treatment 2** at Abu Ali throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
1/6/94	Microalgae	0	0	0	0	0	0	0	4	0	0
	Cladophora	0	0	0	0	0	0	4	0	0	0
	Bryopsis	0	0	0	0	0	0	0	4	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	0	8	0	0	0	0	0	4	0	0
	Padina	0	0	0	0	0	0	0	0	0	8
	Centroceras	0	0	0	0	0	0	0	4	32	16
	Ceramium	0	0	4	0	0	0	0	0	0	0
	Crouania	0	0	0	0	0	0	0	4	4	0
	Polysiphonia	0	12	24	36	4	0	0	4	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0
7/6/94	Microalgae	0	0	8	0	0	0	0	0	0	0
	Enteromorpha	0	0	4	0	0	0	4	4	0	0
	Chaetomorpha	0	0	12	0	0	0	4	8	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	8	12	4	0	0	8	8	4	0	0
	Padina	0	0	4	4	4	0	0	0	4	0
	Hormophysa	0	0	0	0	0	0	0	0	0	4
	Centroceras	0	0	0	0	0	0	0	0	4	0
	Ceramium	0	0	0	0	0	0	0	0	4	0
	Crouania	0	0	0	4	0	0	0	4	0	0
	Spyridia	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	0	8	4	0	0	0	0	12	8	0
12/6/94	*Sphacelaria*	8	4	0	0	0	0	0	0	0	0
	Padina	0	0	0	4	12	0	0	0	0	100
	Ceramium	0	4	0	0	0	0	0	0	0	0
	Spyridia	0	0	0	8	0	0	0	0	0	0
	Polysiphonia	0	0	20	12	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0

2.3.3 (contd.)

Date	Genera	Replicate One Size Class					Replicate Two Size Class				
		1	2	3	4	5	1	2	3	4	5
15/6/94	*Chaetomorpha*	4	0	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	8	20	0	0	0	8	0	0	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Ceramium	0	0	0	0	0	0	8	0	0	0
	Polysiphonia	4	8	24	0	0	12	24	8	0	0
	?Ulvella	4	0	0	0	0	8	0	0	0	0
	Phaeophyte (juv)	0	0	4	0	0	0	0	0	0	0
21/6/94	*Enteromorpha*	0	0	0	0	0	0	0	4	0	0
	Sphacelaria	4	4	4	0	0	0	24	0	0	0
	Padina	0	0	4	8	12	0	0	4	4	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Crouania	0	0	4	4	0	0	0	0	0	0
	Polysiphonia	0	4	20	20	0	12	8	20	0	0
	Phaeophyte (juv)	0	0	4	0	0	0	0	4	0	0
29/6/94	*Enteromorpha*	0	0	0	0	0	0	4	0	0	0
	Chaetomorpha	0	0	4	0	0	0	8	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	4	16	0	0	0	12	8	0	0	0
	Padina	0	0	8	0	0	0	4	0	0	0
	Polysiphonia	8	4	8	20	0	8	36	4	0	0
	Phaeophyte (juv)	0	0	4	0	0	0	0	0	0	0
3/7/94	*Enteromorpha*	0	8	0	0	0	0	0	0	0	0
	Chaetomorpha	0	8	0	0	0	0	0	0	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	0	4	0	0	0
	Sphacelaria	8	4	0	0	0	8	0	0	0	0
	Padina	0	0	0	8	0	0	0	0	4	0
	Hypnea	4	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	8	20	8	0	0	20	60	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
6/7/94	*Enteromorpha*	0	0	0	0	0	0	4	0	0	0
	Chaetomorpha	0	0	0	0	0	0	4	4	0	0
	Sphacelaria	0	4	0	0	0	4	12	0	0	0
	Padina	0	0	0	4	48	0	4	0	16	12
	Polysiphonia	0	8	16	20	0	4	12	16	8	0
10/7/94	*Chaetomorpha*	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	0	0	0	0	0	0	0	0	0
	Padina	0	0	8	8	28	0	0	0	0	0
	Polysiphonia	0	0	0	16	32	0	0	4	32	64
13/7/94	*Chaetomorpha*	0	0	4	0	0	0	0	0	0	0
	Sphacelaria	0	4	0	0	0	0	4	0	0	0
	Polysiphonia	0	8	16	28	40	0	0	8	8	80

2.3.3 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
27/7/94	Microalgae	0	0	0	0	0	8	0	0	0	0
	Enteromorpha	0	4	4	0	0	0	4	4	0	0
	Chaetomorpha	0	0	4	0	0	0	0	0	0	0
	Sphacelaria	16	8	0	0	0	4	16	0	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Hypnea	0	0	0	0	0	0	8	0	0	0
	Ceramium	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	8	20	16	0	0	12	28	0	0	0

2.3.4 Raw data of the algal community growing on the settlement plates in **Treatment 3** at Abu Ali throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
1/6/94	*Chaetomorpha*	0	4	4	0	0	0	0	4	0	0
	Bryopsis	0	0	0	0	0	0	0	0	0	4
	Feld./Hinck.	0	0	0	0	0	0	4	0	0	0
	Sphacelaria	4	8	0	0	0	0	8	12	0	0
	Padina	0	0	0	8	12	0	0	0	4	24
	Hypnea	0	0	4	0	0	0	0	0	0	0
	Centroceras	0	0	4	0	0	0	0	0	0	0
	Crouania	0	0	0	0	0	0	0	4	0	0
	Spyridia	0	0	8	0	0	0	0	0	0	0
	Herposiphonia	0	0	0	0	0	0	0	4	0	0
	Polysiphonia	0	4	28	4	0	0	8	8	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	0	4	0	0
7/6/94	*Enteromorpha*	0	4	0	0	0	0	4	0	0	0
	Chaetomorpha	0	4	0	0	0	0	0	4	0	0
	Feld./Hinck.	8	0	0	0	0	0	0	0	0	0
	Sphacelaria	16	12	12	0	0	4	8	0	0	0
	Padina	0	4	4	0	0	0	0	0	4	4
	Hypnea	0	0	0	0	0	0	4	0	0	0
	Centroceras	0	0	0	0	0	0	0	8	0	0
	Ceramium	0	4	0	0	0	0	0	0	0	0
	Crouania	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	4	4	0	0	0	20	32	0	0
12/6/94	*Enteromorpha*	0	4	0	0	0	0	0	0	0	0
	Chaetomorpha	0	0	4	0	0	0	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	20	20	0	0	0	8	32	0	0	0
	Padina	0	0	0	0	0	0	0	0	20	16
	Hypnea	0	4	0	0	0	0	0	0	0	0
	Chondria	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	4	0	4	0	0	4	8	0	0	0
	?Ulvella	8	0	0	0	0	0	0	0	0	0

2.3.4 (contd.)

Date	Genera	Replicate One Size Class					Replicate Two Size Class				
		1	2	3	4	5	1	2	3	4	5
15/6/94	*Enteromorpha*	0	0	0	0	0	0	4	0	0	0
	Chaetomorpha	0	0	0	0	0	0	4	0	0	0
	Sphacelaria	32	12	0	0	0	32	12	0	0	0
	Padina	0	8	4	0	0	0	0	0	0	0
	Fosiella	4	0	0	0	0	8	0	0	0	0
	Jania	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	0	4	0	0	0	4	8	0	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	8	0	0	0
21/6/94	*Enteromorpha*	0	20	0	0	0	4	0	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	12	12	0	0	0	20	4	0	0	0
	Padina	0	4	4	4	0	0	0	0	4	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	12	12	0	0	0	20	0	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	4	0	0	0
29/6/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Chaetomorpha	0	0	0	0	0	0	4	0	0	0
	Bryopsis	0	0	0	0	0	0	0	0	0	0
	Sphacelaria	4	4	0	0	0	8	4	0	0	0
	Padina	0	8	8	16	0	0	0	12	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Centroceras	0	0	0	0	0	0	4	0	0	0
	Crouania	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	12	4	0	0	16	24	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	4	4	0	0
3/7/94	*Bryopsis*	0	16	4	0	0	0	0	0	0	0
	Sphacelaria	12	4	0	0	0	12	4	0	0	0
	Padina	0	0	0	4	16	0	4	0	0	0
	Hypnea	0	0	0	0	0	4	12	0	0	0
	Polysiphonia	4	32	4	0	0	16	40	0	0	0
6/7/94	*Chaetomorpha*	0	8	0	0	0	0	0	0	0	0
	Bryopsis	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	16	0	0	0	0	4	0	0	0
	Padina	0	0	4	0	0	0	0	0	0	28
	Hypnea	4	20	0	0	0	0	0	0	0	0
	Polysiphonia	16	16	4	0	0	4	52	0	0	0
	?Ulvella	4	0	0	0	0	4	0	0	0	0
10/7/94	*Chaetomorpha*	0	4	0	0	0	0	0	4	0	0
	Sphacelaria	8	12	0	0	0	4	16	0	0	0
	Padina	0	0	0	8	8	0	4	8	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Hypnea	0	8	0	0	0	4	4	0	0	0
	Polysiphonia	16	16	4	0	0	16	24	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0

2.3.4 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
13/7/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Chaetomorpha	0	4	0	0	0	0	8	0	0	0
	Sphacelaria	20	12	0	0	0	0	16	0	0	0
	Polysiphonia	4	32	8	0	0	12	24	0	0	0
	?Ulvella	4	0	0	0	0	4	0	0	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	4	0	0	0
27/7/94	Microalgae	12	0	0	0	0	16	4	0	0	0
	Chaetomorpha	0	4	0	0	0	0	4	0	0	0
	Sphacelaria	0	8	0	0	0	8	12	0	0	0
	Fosiella	4	0	0	0	0	0	0	0	0	0
	Polysiphonia	0	52	0	0	0	4	24	4	0	0
	?Ulvella	4	0	0	0	0	4	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0

2.3.5 Raw data of the algal community growing on the settlement plates in **Treatment 4** at Abu Ali throughout the study period.

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
1/6/94	*Sphacelaria*	0	8	0	0	0	4	16	24	0	0
	Padina	0	0	0	0	4	0	0	0	12	4
	Centroceras	0	0	0	16	4	0	0	0	0	0
	Crouania	0	0	8	4	0	0	0	0	0	0
	Polysiphonia	0	0	16	32	4	0	20	16	0	0
7/6/94	*Enteromorpha*	0	0	0	0	0	0	4	4	0	0
	Chaetomorpha	0	0	12	0	0	4	4	4	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	16	4	4	0	0	8	16	4	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Hypnea	0	0	8	0	0	0	0	0	0	0
	Crouania	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	0	0	8	12	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
12/6/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Enteromorpha	0	0	8	0	0	0	0	0	0	0
	Chaetomorpha	0	0	4	4	0	8	0	0	0	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	8	0	0	0	0
	Sphacelaria	8	4	4	0	0	16	0	0	0	0
	Padina	0	0	0	0	4	0	0	0	0	0
	Polysiphonia	4	8	8	0	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	16	0	0	0	0

2.3.5 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
15/6/94	*Chaetomorpha*	0	4	0	0	0	4	0	0	0	0
	Cladophora	0	0	0	0	0	4	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	16	24	4	0	0	12	0	0	0	0
	Fosiella	4	0	0	0	0	12	0	0	0	0
	Crouania	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	4	4	0	0	0	4	0	0	0	0
	?Ulvella	8	0	0	0	0	20	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0
21/6/94	*Enteromorpha*	4	8	0	0	0	0	4	0	0	0
	Chaetomorpha	0	4	8	0	0	4	4	8	0	0
	Sphacelaria	8	12	4	0	0	20	20	0	0	0
	Padina	0	0	0	0	0	0	0	0	4	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Hypnea	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	12	4	0	0	0	0	8	4	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
29/6/94	*Enteromorpha*	0	8	0	0	0	0	4	0	0	0
	Chaetomorpha	0	4	4	0	0	8	4	0	0	0
	Cladophora	0	0	0	0	0	8	8	0	0	0
	Sphacelaria	8	4	0	0	0	12	0	0	0	0
	Padina	0	0	4	4	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	0	20	16	0	0	4	0	0	0	0
3/7/94	*Enteromorpha*	0	4	0	0	0	4	4	0	0	0
	Chaetomorpha	4	4	0	0	0	4	8	0	0	0
	Cladophora	0	8	0	0	0	8	8	0	0	0
	Bryopsis	0	0	4	0	0	4	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	20	4	0	0	0	8	0	0	0	0
	Padina	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	12	8	0	0	0	4	0	0	0
	?Ulvella	4	0	0	0	0	4	0	0	0	0
6/7/94	*Enteromorpha*	0	0	4	0	0	4	0	0	0	0
	Chaetomorpha	0	0	4	0	0	0	12	4	0	0
	Cladophora	4	8	8	0	0	0	4	0	0	0
	Bryopsis	0	0	0	0	0	4	8	0	0	0
	Sphacelaria	8	4	0	0	0	8	0	0	0	0
	Padina	0	4	0	4	0	0	0	0	0	0
	Fosiella	0	0	0	0	0	8	0	0	0	0
	Hypnea	0	4	0	0	0	0	0	0	0	0
	Crouania	0	4	8	0	0	0	0	0	0	0
	Polysiphonia	8	8	16	0	0	0	12	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0

2.3.5 (contd.)

Date	Genera	Replicate One					Replicate Two				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
10/7/94	*Chaetomorpha*	0	4	4	0	0	8	8	0	0	0
	Cladophora	0	0	0	0	0	8	0	0	0	0
	Sphacelaria	4	0	0	0	0	28	4	0	0	0
	Padina	0	0	0	12	4	0	0	0	0	0
	Fosiella	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	4	24	20	8	0	4	0	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
13/7/94	*Chaetomorpha*	0	8	0	0	0	4	4	4	0	0
	Sphacelaria	8	4	0	0	0	0	0	0	0	0
	Padina	0	0	0	8	8	0	0	0	0	0
	Fosiella	0	0	0	0	0	16	0	0	0	0
	Ceramium	0	4	0	0	0	4	0	0	0	0
	Polysiphonia	0	4	4	16	16	24	0	0	0	0
27/7/94	Microalgae	12	4	0	0	0	0	0	0	0	0
	Enteromorpha	0	12	0	0	0	0	0	0	0	0
	Chaetomorpha	8	4	0	0	0	4	8	0	0	0
	Cladophora	0	0	0	0	0	8	0	0	0	0
	Bryopsis	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	8	0	0	0	0	12	4	0	0	0
	Fosiella	4	0	0	0	0	16	0	0	0	0
	Polysiphonia	8	4	0	0	0	0	0	0	0	0
	?Ulvella	0	0	0	0	0	8	0	0	0	0
	Phaeophyte (juv)	0	8	0	0	0	0	0	0	0	0

2.3.6 Raw data of the algal community growing on the settlement plates in **Treatments 5 and 6** at Abu Ali throughout the study period.

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
1/6/94	*Enteromorpha*	0	0	4	0	0	0	0	4	0	0
	Chaetomorpha	0	0	0	0	0	0	0	0	4	0
	Cladophora	0	4	0	0	0	0	0	0	0	0
	Bryopsis	0	0	0	0	0	0	0	4	0	0
	Feld./Hinck.	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	0	12	0	0	0	4	16	16	0	0
	Padina	0	0	0	0	4	0	0	4	0	0
	Gelidium	0	0	0	0	0	0	4	0	0	0
	Centroceras	0	0	12	4	0	0	0	0	0	0
	Ceramium	0	0	4	0	0	0	0	0	0	0
	Polysiphonia	0	0	36	0	0	0	12	4	4	0
	Phaeophyte (juv)	0	4	0	0	0	0	0	0	0	0

2.3.6 (contd.)

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
7/6/94	*Feld./Hinck.*	0	0	0	0	0	4	0	0	0	0
	Sphacelaria	0	8	0	0	0	16	20	8	0	0
	Padina	0	0	0	0	0	0	0	4	0	0
	Centroceras	0	8	32	0	0	0	0	0	0	0
	Ceramium	0	4	4	0	0	0	0	0	0	0
	Crouania	0	8	0	0	0	0	0	0	0	0
	Polysiphonia	12	8	0	0	0	0	16	8	0	0
12/6/94	*Enteromorpha*	0	0	0	0	0	0	0	12	0	0
	Feld./Hinck.	0	4	0	0	0	0	0	0	0	0
	Sphacelaria	4	8	0	0	0	0	12	4	0	0
	Padina	0	0	0	4	0	0	4	4	4	0
	Hormophysa	0	0	0	0	0	0	0	0	4	4
	Centroceras	0	8	8	0	0	0	0	0	0	0
	Crouania	0	8	8	0	0	0	0	0	0	0
	Herposiphonia	4	0	4	0	0	0	0	0	0	0
	Polysiphonia	4	8	0	0	0	0	20	20	0	0
	Phaeophyte (juv)	4	0	0	0	0	0	0	0	0	4
15/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Chaetomorpha	0	0	4	0	0	4	4	0	0	0
	Cladophora	0	0	0	0	0	8	8	0	0	0
	Cladophoropsis	4	0	0	0	0	0	4	0	0	0
	Sphacelaria	8	20	0	0	0	0	12	0	0	0
	Padina	0	0	8	8	0	0	0	0	0	0
	Hypnea	0	0	0	0	0	0	8	0	0	0
	Polysiphonia	12	4	0	0	0	0	0	0	0	0
	?Ulvella	4	0	0	0	0	12	0	0	0	0
21/6/94	*Enteromorpha*	4	0	4	0	0	4	4	0	0	0
	Chaetomorpha	0	4	4	0	0	0	4	4	0	0
	Sphacelaria	12	4	0	0	0	4	16	8	0	0
	Hormophysa	0	0	0	0	0	0	0	12	0	0
	Herposiphonia	0	4	0	0	0	0	0	0	0	0
	Polysiphonia	4	20	0	0	0	0	8	0	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	0	4	0	0
29/6/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Enteromorpha	0	8	0	0	0	0	0	4	0	0
	Chaetomorpha	0	8	4	0	0	0	0	0	0	0
	Sphacelaria	16	12	0	0	0	12	32	0	0	0
	Hormophysa	0	0	0	0	0	0	0	0	0	8
	Polysiphonia	8	12	0	0	0	4	12	4	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	0	4	0	0

2.3.6 (contd.)

Date	Genera	Treatment Five					Treatment Six				
		Size Class					Size Class				
		1	2	3	4	5	1	2	3	4	5
3/7/94	Microalgae	0	0	0	0	0	4	0	0	0	0
	Enteromorpha	0	4	8	0	0	0	0	0	0	0
	Chaetomorpha	0	0	8	0	0	0	0	4	0	0
	Bryopsis	0	4	0	0	0	0	0	0	0	0
	Feld./Hinck.	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	12	4	0	0	0	12	4	0	0	0
	Padina	0	0	0	0	0	0	0	4	0	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Anotrichium	0	0	4	0	0	0	0	0	0	0
	Herposiphonia	0	0	0	0	0	4	0	0	0	0
	Polysiphonia	8	16	0	0	0	4	28	16	0	0
6/7/94	Microalgae	4	0	0	0	0	0	0	0	0	0
	Enteromorpha	0	0	4	0	0	0	0	0	0	0
	Chaetomorpha	0	8	0	0	0	0	4	0	0	0
	Cladophora	4	4	0	0	0	0	0	0	0	0
	Sphacelaria	16	8	0	0	0	0	16	0	0	0
	Hormophysa	0	0	0	0	0	0	0	0	8	0
	Fosiella	4	0	0	0	0	4	0	0	0	0
	Hypnea	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	0	20	0	0	0	0	32	12	0	0
	?Ulvella	4	0	0	0	0	0	0	0	0	0
10/7/94	Microalgae	8	0	0	0	0	4	0	0	0	0
	Enteromorpha	0	4	4	0	0	0	0	0	0	0
	Chaetomorpha	0	16	8	0	0	0	4	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Feld./Hinck.	0	0	0	0	0	4	4	0	0	0
	Sphacelaria	4	16	4	0	0	4	16	0	0	0
	Padina	0	0	0	0	0	0	4	0	8	4
	Polysiphonia	4	0	0	0	0	12	20	0	0	0
	Phaeophyte (juv)	0	0	4	0	0	0	0	4	0	0
13/7/94	Microalgae	8	0	0	0	0	0	0	0	0	0
	Enteromorpha	0	0	4	0	0	0	4	0	0	0
	Chaetomorpha	0	8	20	0	0	0	4	0	0	0
	Cladophora	4	0	0	0	0	0	0	0	0	0
	Sphacelaria	12	4	0	0	0	0	16	8	0	0
	Ceramium	0	0	0	0	0	0	12	0	0	0
	Polysiphonia	4	4	0	0	0	12	16	4	0	0
	Phaeophyte (juv)	0	0	0	0	0	0	0	4	0	0
27/7/94	Microalgae	8	0	0	0	0	4	0	0	0	0
	Enteromorpha	0	4	0	0	0	0	0	8	0	0
	Chaetomorpha	0	8	20	0	0	0	0	4	0	0
	Sphacelaria	8	20	0	0	0	4	0	0	0	0
	Fosiella	8	0	0	0	0	0	0	0	0	0
	Ceramium	0	0	0	0	0	0	4	0	0	0
	Polysiphonia	8	12	0	0	0	0	32	24	0	0
	?Ulvella	0	0	0	0	0	4	0	0	0	0
	Phaeophyte (juv)	0	4	0	0	0	0	4	0	0	0

Appendix 3

Herbivore Communities

Appendix 3.1 Herbivorous fish

3.1.1 Abundance of herbivorous fish groups recorded along the 50 m transect at **Jana (shallow)**, throughout the study period.

Date	Parrotfish	Rabbitfish	Surgeonfish	Damselfish
12/8/94	28	4	20	11
27/8/94	14	4	10	5
10/9/94	20	6	4	7
21/10/94	27	3	12	6
15/11/94	19	7	14	10
15/12/94	13	8	9	6
29/1/95	12	11	7	11
19/2/95	14	13	12	7
15/4/95	36	3	9	6

3.1.2 Abundance of herbivorous fish groups recorded along the 50 m transect at **Jana (deep)**, throughout the study period.

Date	Parrotfish	Rabbitfish	Surgeonfish	Damselfish
14/8/94	5	0	4	21
27/8/94	12	0	2	24
10/9/94	17	1	7	16
21/10/94	3	0	5	36
15/11/94	5	0	6	26
15/12/94	4	0	3	21
29/1/95	3	0	2	15
19/2/95	2	0	2	20
15/4/95	3	0	11	17

3.1.3 Abundance of herbivorous fish groups recorded along the 50 m transect at **Abu Ali**, throughout the study period.

Date	Parrotfish	Rabbitfish	Surgeonfish	Damselfish
04/07/94	0	73	0	2
06/07/94	0	43	0	3
10/07/94	2	26	0	2
07/08/94	0	81	1	4
10/08/94	0	28	0	3
16/8/94	0	43	1	2
17/8/94	0	65	1	5
18/8/94	0	28	0	4
22/8/94	1	98	0	4
25/8/94	0	83	0	4
28/8/94	1	113	1	7
04/09/94	0	60	0	5
07/09/94	0	53	1	5
11/09/94	0	53	1	3
14/9/94	0	77	0	6
18/9/94	0	68	0	7
25/9/94	2	74	0	0
02/10/94	0	43	0	6
08/10/94	0	28	0	5
15/10/94	0	31	0	2
26/10/94	2	39	1	4
30/10/94	0	21	0	3
02/11/94	1	14	0	7
08/11/94	4	22	1	6
15/11/94	2	36	1	5
23/11/94	1	32	0	6
30/11/94	1	34	0	0
12/12/94	0	0	0	0
05/01/95	0	3	0	0
08/01/95	0	10	0	0
10/01/95	0	35	0	0
11/01/95	0	46	0	0
01/02/95	0	2	0	0
08/ 02/95	0	9	0	0
15/2/95	0	3	0	0
22/2/95	0	20	0	0
26/2/95	0	3	0	0
08/03/95	1	14	0	0
12/03/95	1	20	0	0
20/3/95	1	12	0	0
23/3/95	0	45	0	0
01/04/95	0	11	0	0
09/04/95	0	19	0	0

Appendix 3.2 Herbivorous echinoids

3.2.1 Abundance of *Echinometra mathaei* per 1 m^2 quadrat along the 50 m transect (sampled every 2 m) at **Abu Ali**, throughout the study period.

Date	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48
21/5/94	34	5	5	21	3	16	0	2	3	0	2	8	5	1	16	10	8	3	0	4	4	4	1	4	6
29/5/94	5	8	0	3	8	7	1	0	7	2	14	28	0	7	6	14	3	6	13	1	17	3	4	1	2
1/6/94	26	7	5	20	1	11	1	1	8	6	0	4	5	6	0	16	7	4	1	10	0	4	20	0	0
15/6/94	21	8	8	20	6	10	0	8	10	7	7	11	5	6	11	10	3	5	2	10	4	9	21	2	6
6/7/94	22	5	8	20	6	15	0	4	5	6	4	8	6	3	2	13	3	2	0	6	0	2	11	2	10
10/7/94	21	5	7	21	8	11	0	3	5	2	3	12	5	6	6	7	5	4	1	9	4	9	12	1	13
7/8/94	24	7	10	13	2	11	1	4	8	12	8	8	5	8	5	13	3	7	1	5	2	12	15	0	10
10/8/94	24	6	10	13	2	9	1	3	8	11	3	15	5	6	11	5	5	7	2	8	4	10	12	0	12
18/8/94	18	9	8	20	1	10	0	5	4	8	10	11	4	4	6	17	2	7	3	16	5	16	16	1	11
22/8/94	20	12	8	14	1	12	0	6	7	8	4	16	6	6	14	3	6	6	1	12	0	8	20	1	11
28/8/94	19	10	8	21	3	13	1	11	6	10	5	7	0	9	0	13	3	1	4	3	0	6	9	1	9
4/9/94	19	9	7	20	4	13	1	6	5	3	7	9	13	3	8	14	5	6	2	4	0	10	13	0	7
7/9/94	23	9	9	20	2	11	0	7	5	9	4	4	1	10	1	13	3	1	9	17	1	8	23	0	10
11/9/94	22	7	7	23	0	11	0	8	3	20	5	4	3	10	2	12	3	0	5	14	0	7	20	1	10
14/9/94	26	12	8	24	0	15	0	9	6	13	8	9	0	7	3	7	4	0	8	10	0	5	18	1	12
18/9/94	16	10	7	21	1	10	0	6	5	11	6	8	3	4	2	9	4	0	4	14	2	6	10	2	12
25/9/94	15	10	7	16	2	10	0	8	6	14	5	9	7	6	1	8	4	0	8	14	1	7	17	1	14
2/10/94	14	8	8	10	2	13	0	7	8	14	5	3	6	8	3	14	3	2	5	14	4	8	13	0	19
15/10/94	15	8	8	19	1	10	1	7	5	14	4	2	3	6	0	12	6	2	6	8	1	5	12	2	13
26/10/94	17	7	6	14	1	11	0	9	6	11	4	7	2	3	2	12	5	5	6	6	3	7	13	2	9
30/10/94	15	7	3	17	2	12	1	8	3	11	9	6	3	4	4	9	4	4	5	13	1	5	11	6	10
2/11/94	15	10	4	16	2	12	0	10	5	12	12	6	1	4	1	5	2	1	9	11	4	2	9	2	14
8/11/94	14	8	3	14	2	12	0	7	3	7	10	5	1	4	1	6	3	3	5	9	5	5	8	2	14
16/11/94	10	7	2	13	1	14	1	7	0	2	10	6	1	2	2	8	4	3	9	13	3	4	7	1	10
23/11/94	15	7	2	10	2	10	1	8	7	9	10	10	2	6	4	5	4	2	3	10	5	2	9	2	10
30/11/94	15	8	2	13	2	11	1	7	2	12	5	13	3	8	8	7	4	2	7	15	5	6	9	3	8
12/12/94	7	2	1	7	1	8	1	4	0	1	5	11	1	6	0	3	4	1	5	9	3	3	8	1	5
5/1/95	16	9	3	16	1	18	2	11	3	10	13	17	2	9	3	7	3	2	8	12	6	4	9	2	10
8/1/95	14	10	4	12	1	16	2	7	4	8	13	10	2	5	1	9	2	1	6	10	4	4	8	0	8
11/1/95	14	10	3	10	1	21	1	5	3	8	12	14	0	4	6	12	3	2	4	8	4	4	6	0	10
1/2/95	7	4	3	5	0	9	2	2	1	4	7	11	3	4	1	11	2	1	4	5	1	1	4	0	4
8/2/95	11	8	3	7	1	11	2	0	3	4	5	13	4	6	1	14	1	2	4	0	1	2	2	3	6
15/2/95	8	5	2	5	3	16	1	10	5	4	9	12	2	6	0	11	4	1	4	5	3	1	4	3	6
22/2/95	11	7	4	2	1	13	0	5	3	4	3	10	4	1	1	13	2	1	2	0	1	2	5	0	8
8/3/95	7	4	1	3	3	10	2	5	1	2	3	12	2	5	5	13	2	1	1	2	2	2	1	1	4
12/3/95	9	5	1	7	4	9	1	7	1	2	7	10	1	5	3	18	2	0	2	3	1	4	4	0	3
20/3/95	8	4	1	14	2	11	0	10	2	7	3	14	3	4	4	14	2	2	1	9	0	4	7	0	9
23/3/95	9	7	3	16	4	12	2	12	2	7	6	13	1	5	5	15	2	2	4	8	2	3	6	0	7
1/4/95	12	8	3	12	2	2	1	8	3	6	5	10	4	5	5	14	3	2	3	7	4	2	4	0	9
9/4/95	15	9	3	15	2	14	0	8	3	2	7	9	4	3	5	13	3	2	3	9	4	4	4	0	13

Appendix 4

Echinoid Ecology

Appendix 4.1 Diel gut fullness

4.1.1 Raw data from the diel gut fullness experiment during **summer** (17/8/94).

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	1	55.7	47.5	86.8	66.8	3.469	0.601	0.255	4.642
	2	43.1	41.9	47.4	40.5	2.507	0.540	0.232	4.487
	3	53.8	47.3	77.5	63.5	3.029	0.753	0.304	4.233
	4	50.7	44.1	69.3	56.4	4.01	0.841	0.365	4.87
05:00	5	55.5	45.4	93	70.6	4.148	1.122	0.449	3.547
	6	54.6	45.3	78.8	64.5	2.647	0.523	0.218	3.847
	7	56.5	49.4	95.6	79.1	3.583	0.466	0.220	4.082
	8	53.4	43.6	76.7	59.4	3.12	0.750	0.333	3.897
	9	55.1	44.5	80.5	64.8	3.968	0.855	0.381	5.179
	10	55.5	45.3	80	62.8	3.194	0.595	0.265	3.296
	11	40.5	38.9	36.6	31.4	1.956	0.394	0.179	1.395
	12	60.1	50.9	107.3	86.1	5.709	1.567	0.619	6.792
	13	43.3	37.8	41.6	36	2.294	0.713	0.314	1.86
	14	59.3	50.7	97	74	4.905	1.435	0.605	3.263
09:00	15	61.4	48.8	106.1	80.4	5.452	1.435	0.735	3.704
	16			66.3	57.3	3.836	0.921	0.452	3.285
	17	51.6	44.7	73.3	59	2.969	0.659	0.277	5.506
	18	59.5	48.2	102.7	80.1	3.841	0.653	0.282	4.566
	19			71.2	58.2	4.038	0.820	0.339	2.145
	20	47.5	41.4	54.8	47	3.024	1.135		2.304
	21	61.8	51.5	101.6	75	6.025	1.683	0.751	5.899
	22	53.8	46.2	79.2	64.5	1.985	0.315	0.127	4.384
	23	54.5	46.1	85.9	70.6	4.281	1.127	0.477	4.509
	24	60.1	49.5	100.7	78.1	3.935	0.966	0.436	4.18
13:00	25	61.5	54.2	100.1	79.1	5.446	1.257	0.709	5.255
	26	55.1	46.9	84.7	68.7	6.147	1.671	0.679	3.346
	27	53.8	44.4	68.8	56.8	3.918	1.179	0.469	4.136
	28	55.3	47.6	90.3	74.7	5.528	1.437	0.631	4.244
	29			88.1	69.5	4.51	1.066	0.424	5.267
	30	54.9	41.3	77.1	59.9	3.238	0.594	0.235	4.157

4.1.1 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	31	54.2	47.8	85	67.8	4.53	0.905	0.588	2.508
	32	53.1	44.9	79.8	66.8	4.121	1.185	0.787	3.775
	33	58.6	46.8	89.3	70.3	5.676	1.353	0.561	3.787
	34	59.7	52.5	105.4	82.5	5.263	1.386	0.889	5.487
17:00	35	55.9	47	81.5	64	3.965	0.782	0.333	3.845
	36	50.2	41.8	67.1	55.9	4.133	1.089	0.461	3.072
	37	61	48.3	99.9	79.7	5.979	1.132	0.510	3.435
	38	55.5	48.2	81.3	66.8	3.665	0.704	0.458	2.796
	39	59.4	51.1	106.4	81.3	3.196	0.335	0.120	4.515
	40	50.2	43.1	66.8	56.7	3.154	0.879	0.711	4.4
	41	60.9	52.4	107.6	89	6.474	1.746	0.820	10.883
	42	56.5	47.5	85.7	71.1	5.683	1.612	0.696	5.18
	43	60.1	52.2	105.2	81.5	4.484	0.753	0.423	5.752
	44	58	48	98.5	78.5	5.012	0.913	0.476	5.911
21:00	45	52.3	43.9	75.3	59.5	1.822	0.127	0.054	3.155
	46	57.8	48.1	97.2	78.4	6.283	1.691	0.785	4.865
	47	53.2	45	85.5	71.3	4.82	1.239	0.571	4.14
	48	54.4	44.8	91.5	75.1	4.768	1.225	0.495	6.907
	49	60.9	52.3	100.9	79.5	4.347	0.998	0.423	4.659
	50	59.1	50.1	93.2	74.3	5.753	1.426	0.650	5.205
	51	55.1	49.4	88.4	69.8	5.339	1.615	1.492	3.752
	52	59.3	48.8	91.8	70.9	4.501	0.764	0.633	3.747
	53	51.3	43.8	76.6	62.3	3.879	0.992	0.874	3.448
	54	57.8	52.5	106.1	81.3	6.531	1.169	0.977	6.012
01:00	55	50.5	42.8	69	58.7	3.552	0.834	0.728	3.73
	56	57.8	47.8	91.1	76.6	3.915	1.057	0.953	2.84
	57	45	37.3	48	41.5	1.836	0.365	0.310	2.923
	58	58.9	49.7	99.8	75.8	5.035	0.816	0.671	2.514
	59	58.4	45.5	91.2	75.7	4.971	0.904	0.769	6.215
	60	59.4	50.1	94.6	72.2	4.691	1.456	1.337	4.222

4.1.2 Raw data from the diel feeding experiment during **winter** (10/1/95).

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	1	63.5	52.8	126.3	103.8	10.427	2.495	1.334	10.321
	2	65.8	54.3	131.2	112.5	10.806	2.387	0.990	12.416
	3	56.4	48.5	87.4	75.8	7.866	2.275	1.308	7.067
	4	59.5	47.9	92.7	81.9	8.883	2.195	0.807	5.046
07:00	5	60	50.9	104.7	90.3	10.787	2.775	1.358	6.022
	6	60.8	50.5	125.6	105.9	9.863	3.031	1.679	5.466
	7	54.6	45.6	84.3	72.5	8.629	2.089	0.942	3.652
	8	50	43.5	67.5	57.6	4.998	1.225	0.653	4.175
	9	44.4	37.3	50.6	48.3	4.265	1.087	0.528	
	10	50.6	44.3	73.1	67.2	8.486	1.910	0.719	4.366
	11	59.3	49.7	99.8	84.3	7.676	2.499	0.969	4.663
	12	42.5	33.4	43.4	39.7	4.083	1.333	0.850	1.313
	13	55.1	48.9	96	79.1	8.171	1.807	0.453	3.752
	14	55.7	45.8	99	82.9	10.367	3.128	1.336	3.076
11:00	15	60.3	47.7	101.6	82.6	9.363	3.188	1.051	6.088
	16	62.2	54	109.6	91.9	8.478	2.582	0.964	10.485
	17	61.5	53.9	109.5	90.2	9.563	2.985	1.324	6.036
	18	60.2	51.1	110.4	91.7	9.112	3.058	1.442	6.912
	19	47.5	39.7	59.2	54	5.947	1.731	0.760	1.784
	20	48.4	42.2	58.8	49.7	5.143	1.452	0.541	1.521
	21	59.8	49.8	105.4	85.3	8.833	2.496	0.903	6.662
	22	55	47.1	93.1	78	6.757	1.865	0.562	4.449
	23	55.2	47.7	84.2	70.8	7.258	2.510	0.745	4.041
	24	51.4	43.8	70.6	60.4	5.78	1.959	0.544	4.514
15:00	25	42	34.8	41.1	37	5.143	1.849	0.544	1.393
	26	53.6	44.5	83.8	72.6	6.819	2.048	0.710	4.404
	27	57.8	49.3	94.7	79.9	8.594	2.700	0.838	3.718
	28	57.3	45	95.7	77	7.102	1.501	0.417	3.611
	29	49.4	41.8	64	57.6	5.16	1.471	0.608	5.418
	30	48.5	46.8	67.2	57.8	5.678	1.517	0.489	2.634

4.1.2 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	31	55	45.1	88.5	75.1	9.378	2.718	0.876	3.324
	32	56.2	49	83	69.6	7.335	2.445	0.674	5.612
	33	53.3	46.1	86.1	70.7	7.186	2.257	0.659	4.305
	34	52.7	45.3	87.6	73.8	7.133	2.547	0.763	3.73
19:00	35	53.8	44.3	77.9	66.5	6.681	1.877	0.582	3.393
	36	57.9	48	93.9	78.5	7.899	1.995	0.646	4.343
	37	59.4	49	103.7	87.6	8.545	1.761	1.032	8.052
	38	55.7	49	89	75.3	7.222	1.858	0.987	3.594
	39	58.8	50.8	93.9	79.1	7.888	2.362	0.824	5.631
	40	49	42.1	68.6	60.4	6.984	2.157	0.687	3.404
	41	55	45.6	87.6	74.9	8.647	2.750	1.006	4.397
	42	54.5	48.2	92.6	76.8	7.65	2.682	0.871	5.947
	43	55.5	43.7	80.2	67.1	7.598	1.967	1.145	3.818
	44	50	41.4	74.5	66.7	7.134	2.182	1.239	4.053
23:00	45	32.1	29.2	23.6	21.4	2.246	0.562	0.228	(none)
	46	56.2	48.9	94.4	76.1	10.098	3.815	1.309	2.569
	47	53	45.2	83.5	69.4	7.228	2.444	0.824	2.915
	48	55.1	45.4	88	76.6	7.032	1.727	0.888	7.832
	49	53	45.8	74.9	64.1	7.775	2.540	1.294	3.455
	50	50.2	41.4	65.7	56.8	4.808	1.247	0.594	2.369
	51	57.4	47.7	97.9	79.9	7.217	1.711	1.001	4.104
	52	54	45.5	96.7	84.4	7.039	1.765	1.263	7.415
	53	55.2	47.2	90.9	80.3	8.719	2.387	1.311	8.479
	54	56.5	46.1	90.3	75.2	6.58	1.606	0.936	6.113
03:00	55	47.4	39.8	65.6	59.3	6.56	1.979	1.358	4.24
	56	56.2	47.9	98.8	82.7	8.034	1.795	1.182	5.436
	57	60	51.5	113.6	94.4	8.682	2.627		7.508
	58	56.4	48.3	95.9	80.2	7.179	1.831	1.325	4.165
	59	50	41.7	66.3	59.7	5.424	1.324	0.913	5.063
	60	36.6	30.5	32.6	31.4	2.679	0.796	0.582	1.89

Appendix 4.2 Gut evacuation and bioerosion

4.2.1 Raw data from the gut evacuation experiment during **summer** (16/8/94).

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	1	51.2	40.7	66.8	56.9	3.338	0.629	0.502	3.836
	2	58.1	48.1	89.8	71.8	4.417	0.576	0.391	4.469
	3	50.4	43.5	73.9	59.2	3.728	0.885	0.729	2.921
	4	58.5	48.8	95.6	69.7	4.29	1.128	0.409	3.404
05:00	5	50.6	41.5	60.5	50.3	3.124	0.663	0.478	4.4
	6	61.8	50.3	106.7	87.2	6.838	2.499	0.906	4.127
	7	59.3	48.5	103.8	79.9	6.466	1.480	0.588	3.344
	8	57.4	48	88.8	68.2	2.868	0.497	0.349	5.405
	9	58.5	52	94.2	74	6.263	1.791	0.601	1.905
	10	59.5	47.7	91	72.3	1.965	0.152	0.044	6.747
	11	58.3	49.7	88.6	66.5	4.947	0.622	0.319	3.18
	12	58.7	48.9	89.3	68.1	3.884	0.631	0.492	3.012
	13	60.2	48.8	93.9	72.2	5.437	1.064	0.908	2.457
	14	55	48.1	90.9	71.9	4.182	0.690	0.505	2.632
06:00	15	50.4	38.8	63.5	51.9	4.475	0.925	0.752	2.73
	16	66.6	54.3	128.8	92.9	4.08	0.772	0.602	8.06
	17	60.3	51.3	102.2	77.4	4.999	0.903	0.675	5.656
	18	58.9	49.7	87.1	69	3.672	0.579	0.319	4.333
	19	56.5	46.9	89.5	70.6	2.914	0.388	0.262	4.742
	20	42.1	36.2	40	35.3	1.396	0.236	0.200	3.543
	21	60.5	50.8	104.3	81.5	4.231	0.896	0.639	3.872
	22	60.2	52.3	111.9	88.9	4.52	0.760	0.582	4.454
	23	55.2	46.8	86.2	74	4.048	0.968	0.765	8.114
	24	56.3	43.7	70.1	56.6	3.388	0.933	0.301	2.81
07:00	25	54.5	43.3	73.1	59.8	3.653	0.650	0.514	3.856
	26	60.9	50.6	103	81.2	3.765	0.637	0.284	5.643
	27	61.4	53	108.2	82.2	5.21	1.301	1.097	3.894
	28	60.5	49.2	94.6	71.9	2.833	0.380	0.226	5.662
	29	57.9	51	96.7	77.7	5.572	0.941	0.519	4.059
	30	47.4	41.2	59.3	52.1	2.933	0.548	0.420	3.545
	31	54.3	47.6	82.6	63.3	3.755	0.860	0.303	2.112
	32	57.8	48	97.9	75.2	3.994	0.962	0.315	1.99
	33	56.6	48.6	84.7	67.6	3.506	0.795	0.661	3.709
	34	55.4	44.6	84.5	68.7	3.261	0.559	0.420	3.82
08:00	35	51.1	42.9	68.5	54.3	3.242	0.780	0.681	2.927
	36	62.1	51.8	122.1	94.3	3.6	0.544	0.444	7.321
	37	58.3	49.8	97.7	74.8	4.186	0.743	0.615	3.272
	38	60.5	50.4	98.2	73.3	4.969	1.132	0.953	2.551
	39	48.2	42	60.8	50	3.868	0.697	0.536	1.512
	40	48	42.3	60.9	45.3	1.804	0.217	0.168	1.37

4.2.1 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	41	55.4	45.4	84.3	68.1	4.573	1.559	0.572	2.857
	42	60.3	50.6	101.5	83.4	4.33	0.747	0.478	5.48
	43	55	44.3	82.2	67.1	3.379	0.687	0.566	4.257
	44	55.9	45.3	77.6	63.8	3.056	0.389	0.291	3.412
10:00	45	55.9	47	86.3	72.3	3.626	0.600	0.345	5.169
	46	57.1	47.3	92.8	76.4	4.649	1.182	0.920	2.835
	47	58.6	49.8	98.4	80.4	4.245	0.810	0.697	4.428
	48	52.6	44.2	88.1	72.5	2.765	0.283	0.170	2.592
	49	59.1	50	97.1	78	2.659	0.293	0.170	3.852
	50	49.3	42.4	62.1	49.5	2.208	0.352	0.266	1.883
	51	65.2	55.3	126.7	93.1	6.06	1.042	0.831	5.046
	52	56.2	48.8	94.1	73.7	3.258	0.469	0.341	3.917
	53	53	45.2	75.5	57.8	3.206	0.591	0.461	2.403
	54	52.1	43.7	72	56.7	2.75	0.416	0.301	2.552
12:00	55	40.9	36.5	39.8	33.8	1.642	0.196	0.126	1.111
	56	51.4	44.1	76	58.1	2.706	0.524	0.420	3.016
	57	54.8	44.6	79.1	63.9	2.663	0.515	0.375	5.841
	58	50.3	39.8	66.6	53.8	3.603			2.638
	59	50	38.7	60	48.9	1.942	0.169	0.117	3.056
	60	41.7	35.5	39.9	33.6	2.039	0.313	0.174	1.315
	61	56.6	48.9	91.8	72.2	4.08			3.726
	62	57.4	45.7	93.6	70.7	2.414			4.309
	63	55	46.5	80.1	63.8	2.927			4.289
	64	54.8	45.1	88.4	68	4.481			3.23
14:00	65	61.4	53.1	100.5	75.1	5.742			3.289
	66	59.1	47.3	106.7	83.3	3.017			5.415
	67	58.4	49.3	100.8	81.9	3.605			6.091
	68	54.4	43.4	70.3	56.3	3.129			3.427
	69	54.7	43.6	69.4	53.5	2.923			2.759
	70	41.1	34.7	38.4	32.8	1.285			1.411
	71	51.8	47.3	80.8	61.8	2.769			2.142
	72	59.9	48	94	74.1	4.381			3.21
	73	58	48.9	105.5	81.7	2.476			4.754
	74	60	48.5	99.3	76.9	3.338			5.686
17:00	75	56.9	49	88.3	69.9	2.995			4.029
	76	56.9	49.3	96.4	78	3.359			3.772
	77	59.8	50	115.8	92.2	3.059			3.776
	78	60.4	48.2	111	83.2	3.759			2.555
	79	59.4	48.5	100.6	79.6	2.938			5.667
	80	53.1	44.3	82.5	65.2	3.185			3.989

4.2.1 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	81	56.6	47.4	92.3	72.5	3.909			1.773
	82	59.6	49.9	103	81.1	3.684			6.007
	83	56.8	45.4	90.4	72.8	3.138			2.94
	84	52.5	42.8	80.6	64.2	2.056			5.374
21:00	85	49.8	41.9	64	50.7	1.878			1.66
	86	59.5	51.6	97.8	74.4	2.784			4.106
	87	57.2	43.5	89	67.6	2.315			3.759
	88	58.3	50.3	93.8	68.3	5.124			2.182
	89	50.9	43.8	65.7	51.4	2.004			2.471
	90	53	46.1	85.7	70.5	3.145			4.193
	101	55.9	46.8	87.5	68.5	1.335			1.772
	102	57.4	48.3	87	66.9	3.506			2.437
	103	57.4	49.7	85.4	61.7	2.912			1.776
	104	50.2	42.8	70.2	56.6	1.658			2.74
05:00	105	52.9	44.9	71.9	57.1	1.414			3.212
	106	61.1	48.2	104.6	80.8	2.799			4.412
	107	62.2	52.8	120.4	92.1	3.989			7.28
	108	55.6	48.3	92.6	72.4	2.492			3.889
	109	55.4	45.9	93.8	74.6	2.669			3.413
	110	42.1	36.5	40.1	35.8	0.72			3.239
	111	61.7	51.3	102.4	68.8	2.546			1.994
	112	56.8	47.9	93.7	72.1	1.992			2.267
	113	58	46.9	95.1	77.5	3.986			4.225
	114	52.2	48.5	72.5	54.8	1.227			2.144
10:00	115	52.5	43.7	65.8	53.5	2.28			4.803
	116	59.9	52.6	106.9	77.3	1.986			2.864
	117	56	46.8	94.2	74.6	2.888			5.178
	118	55.6	46.5	93.3	75.6	3.12			4.268
	119	51.6	43.4	77.7	60.8	1.781			3.545
	120	53.9	44.3	78.9	61.4	1.48			2.814
	121	56.4	46.8	87	64.3	1.459			3.677
	122	54.5	43.7	79.6	57.7	2.392			2.038
	123	55.9	42.8	85.9	66.2	2.238			3.699
	124	50.1	44.3	72.5	57.9	1.195			2.606
15:00	125	56.5	46.6	81.8	60.1	1.156			2.227
	126	62.2	51.8	109	86.6	3.802			5.284
	127	62.3	50.6	116.3	86.5	3.523			4.853
	128	56.9	48	93.7	77.4	1.9			4.994
	129	55.9	47.1	82.3	62	2.546			2.337
	130	38.2	33.5	31.2	26.8	0.897			1.481

4.2.1 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	131	59.9	53	106.5	83.6	3.43			4.696
	132	57.9	47.4	100.2	78.1	2.341			4.43
	133	55.6	48.1	88.5	67.3	1.944			3.616
	134	54.5	43	70.3	53.7	1.878			3.242
20:00	135	49.7	39.9	55.1	43.5	1.692			1.703
	136	54.5	48.9	90.4	69.8	1.404			3.665
	137	50.8	44.1	70.2	57.6	2.51			4.323
	138	57.2	46.2	82.9	60.9	1.602			5.502
	139	56.5	46.4	83.4	60.4	1.709			1.862
	140	49.8	39.5	56.6	45.3	1.428			2.652
	141	63.6	54.4	118.8	83.2	1.824			3.025
	142	58.1	50.3	94.7	71.6	1.94			3.092
	143	53.8	44.7	85.9	65.8	1.475			2.758
	144	58.1	49.4	92.2	66.9	3.074			1.82
01:00	145	41.9	34.1	37	31.2	0.511			1.243
	146	54.6	43.6	77.9	62.2	1.41			3.549
	147	57.6	48.4	86.7	60.8	1.949			1.532
	148	59.4	48.3	98.6	76.8	3.014			4.417
	149	60	49.7	102.5	78.1	3.933			5.106
	150	53	39.4	62.7	49.2	1.947			2.832
	151	59.5	48	100.4	77.2	1.359			4.795
	152	55	45.9	83.5	70.6	2.266			9.531
	153	53.4	43.3	69.1	55.3	1.582			2.463
	154	52.5	45.4	70.7	52.5	1.169			2.021
06:00	155	55	42.7	77.9	57.7	1.285			4.579
	156	58.3	48.3	97.4	76.4	1.437			3.414
	157	50.4	44.6	67.5	51.9	1.594			2.277
	158	59.1	48.5	85.7	60.3	1.747			1.788
	159	44.1	35.7	46.3	37.7	1.399			1.873
	160	38.8	31.5	33	29.3	1.307			1.151
	161	58.7	50.5	97.7	71.6	2.409			3.118
	162	56.4	47.5	87.2	68.4	1.25			5.192
	163	52.8	43.6	75.5	58.9	1.01			2.31
	164	46.7	34.3	49	40.3	1.303			1.043
11:00	165	38.5	32.8	31.6	26.3	0.57			1.273
	166	54.3	44.1	85.1	64.5	1.267			1.448
	167	53.7	44.8	72.2	59.1	2.184			4.317
	168	54.7	46.8	77.8	59.3	1.149			1.531
	169	55.5	48	76.3	58.1	1.362			2.209
	170	51.7	44.2	67.5	53.6	0.903			3.327

4.2.2 Raw data from the gut evacuation experiment during winter (10/1/95).

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	1	57.7	48.5	112.6	89.8	9.359	2.763	1.459	3.954
	2	55.8	46.6	99	83.6	9.438	2.692	1.368	4.582
	3	57.7	50.2	95.3	78.5	9.193	2.817	1.494	4.988
	4	50	40.7	62.4	55.5	5.878	1.476	1.032	5.881
07:00	5	40.8	34.4	43.7	40.8	4.087	1.407	0.852	3.35
	6	53.6	44.3	83.7	69.6	6.693	2.100	1.071	3.655
	7	56.4	45.8	98.5	83.2	9.624	3.259	1.406	4.361
	8	52.2	42.3	77.1	66.5	6.763	2.202	1.257	3.709
	9	50.7	44.5	78.1	68.4	5.628	1.404	0.868	4.95
	10	51.2	43.4	79.6	67.3	6.793	1.692	1.029	3.901
	11	59.8	52.5	114.6	93	8.544	2.403	0.892	8.79
	12	63.4	51.3	101.1	85.6	8.5	2.119	1.009	10.112
	13	53.1	48	90.4	79.4	8.34	2.110	0.895	10.076
	14	54	44.4	85.4	76.2	6.698	1.810	0.994	8.797
08:00	15	57.6	46.8	77.8	65.3	5.572	1.364	0.824	8.734
	16	55.8	57.1	87.7	76.3	8.087	2.558	1.197	8.56
	17	52.6	44.3	74.9	65.2	5.57	1.584	0.929	6.992
	18	55.8	48.1	90.6	78.9	9.215	3.027	1.356	7.225
	19	52.8	43.7	71.3	62.3	6.328	1.818	1.023	7.666
	20	44.3	37	49.2	44.5	4.259	1.231	0.899	5.837
	21	55.8	46.3	88.3	75.3	6.736	1.619	0.988	4.867
	22	55.3	45.3	95.4	80.5	9.243	2.647	1.376	3.058
	23	56.5	49.4	93.9	75.3	8.646	2.245	1.095	6.018
	24	54.1	48.5	82.3	70.8	7.005	1.401	0.901	5.712
09:00	25	49.6	41.8	59.8	52.6	5.705	1.534	0.768	4.164
	26	57.3	48.2	98.2	76.8	8.442	2.320	1.364	5.441
	27	58.5	46.5	104.3	82.8	9.174	2.643	1.739	5.608
	28	50.8	42.9	76.8	67.7	7.186	1.928	1.197	5.503
	29	54.6	45.3	79.2	69.5	6.953	1.581	1.158	5.892
	30	49.3	40.7	66.7	58.4	4.438	1.203	0.563	6.634
	31	60.8	51.4	100.4	82.7	8.616	2.618	1.306	8.245
	32	59.3	49.5	93	78.9	7.697	2.047	1.180	8.279
	33	57	48.5	82.6	69.6	6.659	1.940	1.133	6.486
	34	54.5	46.5	84.4	77	7.512	2.209	1.101	8.916
10:00	35	50.8	42.5	70	62.6	6.036	1.802	0.910	5.003
	36	55.2	48.5	94.6	78.6	8.18	2.183	1.347	7.496
	37	57.6	48.3	90.7	71.3	7.45	2.304	1.281	3.728
	38	56	47.4	91.8	75.7	8.791	2.679	1.697	4.114
	39	50.4	43	62.2	55.6	5.569	1.335	0.713	5.167
	40	40	34.8	41.5	38.5	4.322	1.229	0.714	2.619

4.2.2 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	41	55	45.4	87.8	74.2	7.473	2.174	1.120	6.193
	42	59.2	49.9	102.6	81.6	9.787	2.806	1.988	5.62
	43	56.3	46.8	92.6	77.8	6.238	2.165	1.023	4.547
	44	58.1	50.1	92.2	75.8	8.541	2.795	1.409	8.892
12:00	45	56.5	47.8	86.4	73.2	5.793	1.558	0.647	8.797
	46	55.4	47.9	86.7	69.1	5.722	1.216	0.610	6.31
	47	53	45.5	93.9	73.6	5.863	1.291	0.605	5.243
	48	52.2	43.6	77.9	66.9	5.468	1.338	0.639	5.068
	49	56	48.1	85.1	71	5.416	1.265	0.656	6.795
	50	55	45.8	82	70.3	6.315	1.817	1.244	4.83
	51	57.6	45.3	84.9	68.4	8.003	2.253	1.465	4.562
	52	59.2	49.8	90.7	75.1	8.003	1.970	1.218	7.495
	53	57	49	87.2	72.6	8.127	2.259	1.355	6.573
	54	55.7	48.5	95.3	76.4	7.078	1.759	0.688	4.829
14:00	55	57	47.9	88.4	66.8	4.393	1.024	0.706	4.922
	56	55.7	45.9	90	74.7	5.73	1.627	1.208	5.601
	57	52.8	44.8	74.4	64.8	5.392	1.299	0.799	5.253
	58	54.2	44.3	72.9	57.6	5.957	1.598	0.668	5.662
	59	52.3	43	73.5	61.9	7.434	2.016	1.215	5.084
	60	45	41.7	56.7	51.1	6.912	2.027	1.031	2.642
	61	58.6	47.9	91.1	71.6	5.602			5.901
	62	55	46.2	90.9	72.5	6.388			4.699
	63	60.2	48	103.4	82.8	9.307			8.555
	64	54.3	44	79.5	66.7	8.01			4.888
16:00	65	42.7	34.2	40.7	37.4	3.386			2.798
	66	56.3	48.2	95.2	78.6	5.957			5.985
	67	60	48.5	92.5	76.2	8.55			7.518
	68	57.5	49.3	98.1	79.6	8.635			7.936
	69	58	46.5	95.2	79.1	7.79			7.46
	70	51.6	43.2	70	60.6	6.232			3.949
	71	60	49.3	95.5	78.3	6.566			6.465
	72	56.9	48	95.2	77.4	6.788			7.442
	73	54.6	45.9	88.6	73.3	7.602			5.359
	74	55.8	44.4	84.7	72.4	8.441			5.594
19:00	75	50	43	71.7	63.1	4.41			8.058
	76	55.5	49.2	97.3	79.4	7.064			6.008
	77	58.2	52	116.3	92	7.746			5.056
	78	54.7	47.7	93.4	82.2	7.622			4.547
	79	51.1	44.5	77.3	65.9	7.141			3.408
	80	37.2	31.5	35.4	33	3.435			2.044

4.2.2 (contd.)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
	81	55.8	47.2	100.9	82.2	6.807			7.1
	82	60.2	62.8	105	84	9.36			7.973
	83	55	48.3	91.8	78	6.461			5.212
	84	54.8	46.2	88	73.9	9.398			3.968
23:00	85	51.1	43.1	76.3	68	5.709			4.84
	86	56.2	46	96.1	79.6	7.256			8.009
	87	52.7	44.9	86.1	73.7	6.731			4.705
	88	52.6	42.8	75.4	65.5	5.454			6.07
	89	54.3	44.1	80.3	66.3	4.869			6.682
	90	48.7	40.8	56.3	49.1	5.704			4.455
	101	55.4	46	85.9	73.8	7.936			6.759
	102	54.1	44.8	85	74.1	5.093			8.132
	103	57.5	46.6	97.1	80.8	7.953			8.914
	104	49.4	44	73.1	61.5	5.755			4.344
07:00	105	47.6	39	61.6	56.8	5.239			5.63
	106	51.6	42	83.8	71.7	6.506			4.74
	107	51.5	43.7	86.6	75.4	7.588			5.089
	108	50.1	43.5	75.9	66.2	5.393			6.503
	109	55	42.8	82.4	70.4	6.056			7.18
	110	40.8	33	41.2	37.7	2.922			2.284

Appendix 4.3 Bioerosion vs. sedimentation

Raw data from the bioerosion vs. sedimentation experiment, where; (a) initial diurnal gut fullness, (b) after five days starvation, (c) after five days of gut filling in two treatments; caged settlement plates and open reef substrate.

(a)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
10:45	1	60.2	50.2	104.4	86.4	13.227	0.934	0.309	5.232
	2	53.1	45.6	85.6	75.9	8.767	0.954		5.403
	3	59	51	93.3	79.9	11.002	0.714	0.233	6.685
	4	56.1	47.6	99.9	86.6	12.08	0.928	0.205	5.104
	5	56.4	45	89.8	79.7	8.683			7.134

(b)

Time	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
12:00	1	55.8	46.4	99.1	82.7	6.319	0.432	0.170	4.328
	2	55.3	44.7	85	70.1	4.032	0.593	0.397	7.597
	3	51.6	44.8	85.5	62.3	5.704	0.400	0.130	2.778
	4	55	45.7	85.3	72.6	5.735	0.514	0.169	6.402
	5	39.7	34.4	36.1	31.4	1.633	0.192	0.096	1.891

(c)

Treat.	Sample No.	Diameter (long)	Diameter (short)	WB Wt (g)	DB Wt (g)	WG Wt (g)	DGC Wt (g)	CaCO3 Wt (g)	WGd. Wt (g)
R1:T1	1	55.6	46	91	78.2	9.846	3.080	1.132	5.469
	2	50.4	43.6	79.6	70.3	9.627	2.726	0.965	6.348
	3	47.7	38.8	62.3	56.2	7.433	2.117	0.745	3.833
	4	48.5	39.8	56.5	47.4	7.947	2.620	0.991	1.133
	5	41.4	34.2	37.4	34	4.364	0.882	0.293	1.474
R1:T5	6	57.9	50	93	79.2	12.469	4.042	1.485	2.692
	7	58.2	49.4	106	92.9	9.081	3.180	1.202	11.948
	8	56	47.4	99.1	87	9.737	3.176	1.144	9.7
	9	51.6	43.6	70.4	60.2	8.019	2.922	1.106	3.278
	10	40.5	34.6	36.4	33.6	4.063	1.194	0.457	3.169
Reef	1	56.3	49.5	93.7	75.5	9.177	2.305	1.405	5.267
	2	57	43.5	85.3	68.8	8.232	1.360	0.475	1.984
	3	53.5	44.5	83.4	71.6	8.192	1.964	0.704	3.868
	4	55.3	49.8	82.2	69.2	8.002	2.011	0.762	3.847
	5	54	44.4	83.9	72.9	9.86	2.374	1.230	5.717
	6	54.3	47	83.2	71.8	8.689	2.375	1.009	5.476
	7	35.4	32.5	28.9	27				

Appendix 4.4 Diurnal foraging behaviour

4.4.1 Raw data for the diurnal foraging behaviour experiment during **summer** (17/8/94).

Behaviour:		*None*		*None*		*Open*	
Time:	**No.**	**Bearing**	**Distance**	**Bearing**	**Distance**	**Bearing**	**Distance**
05:30	**1**	5	29.5	270	26.5	110	41
	2	15	36.5	275	34.5	100	26.5
	3	10	44	280	38	85	34.5
	4	350	42	290	39.5	60	26
	5	340	38.5	295	42.5	45	30
	6	0	37	300	36	170	48
06:30	**1**	46	40	270	25	115	41.5
	2	30	58	270	32.5	95	28
	3	15	58	280	39.5	85	36.5
	4	355	44	290	36	65	27.5
	5	340	44.5	295	43	40	31.5
	6	15	48.5	5	38	165	49
07:30	**1**	15	52	260	23.5	115	43.5
	2	20	58	270	28.5	100	28
	3	0	80.5	260	32.5	90	36.5
	4	355	43	290	42.5	60	28.5
	5	330	42.5	300	38.5	40	32.5
	6	355	60	285	27.5	170	50
08:30	**1**	340	70	250	27.5	115	41.5
	2	20	65.5	240	26	105	28.5
	3	0	84.5	250	31	90	35.5
	4	0	44.5	260	37	55	28
	5	350	43	290	35	40	32
	6	355	74.5	285	26.5	165	49
09:30	**1**	340	61.5	235	20	120	40
	2	20	69	245	24	105	26.5
	3	355	85.5	290	17.5	90	34
	4	15	61.5	270	40.5	60	28
	5	350	40	300	33	50	33
	6	0	79	300	24	170	48
10:30	**1**	340	61	265	34	115	41
	2	115	68	250	24.5	105	29.5
	3	0	95.5	345	21	90	35
	4	0	52	270	34	60	28
	5	5	42	290	31	45	32.5
	6	10	81	300	25	170	49
11:30	**1**	320	67	260	32.5	115	40.5
	2	340	82.5	265	25.5	110	28.5
	3	115	107	225	18.5	85	24.5
	4	30	58.5	270	30.5	60	27
	5	55	34	290	25.5	50	34
	6	10	77	300	24	170	49

4.4.1 (contd.)

Behaviour:		*None*		*None*		*Open*	
Time:	**No.**	**Bearing**	**Distance**	**Bearing**	**Distance**	**Bearing**	**Distance**
12:30	**1**	320	73	260	33	110	41.5
	2	350	32	265	25	105	26.5
	3	5	86	310	28.5	90	30
	4	320	64.5	270	29	55	27.5
	5	50	29	285	27	40	36.5
	6	10	77.5	300	15	165	48.5
13:30	**1**	320	76.5	250	19.5	120	42
	2	340	40	240	26.5	120	37
	3	10	113	225	15.5	0	3
	4	335	40	315	27.5	65	29
	5	5	48.5	270	33	40	31
	6	20	81.5	250	31.5	170	48.5
14:30	**1**	5	55	240	31	115	41.5
	2	330	35	250	22	115	36
	3	15	100	305	27	0	0
	4	295	39.5	270	26	60	29.5
	5	50	36.5	240	15.5	65	36
	6	15	55	340	33.5	165	48
15:30	**1**	30	79	250	32	110	41.5
	2	325	23.5	250	24	110	36
	3	15	117.5	315	30	180	2
	4	290	42	275	27	60	30.5
	5	50	38.5	255	17.5	75	39
	6	5	50.5	15	46.5	170	49
16:30	**1**	5	103.5	250	30	110	40
	2	255	28	250	22.5	120	36
	3	115	135	270	29	190	14
	4	250	38.5	310	28	55	29.5
	5	40	51	240	15	60	24
	6	350	29.5	285	33.5	170	48.5
17:30	**1**	20	102	240	13.5	120	40
	2	285	24.4	245	22	120	36
	3	10	128	310	27	240	2
	4	220	29.5	250	16	60	31
	5	25	58	245	29	40	18
	6	295	33.5	265	24	170	45
18:30	**1**	20	137	210	17.5	120	41
	2	290	25	250	23	120	36
	3	0	128	310	28	270	2
	4	280	29.5	255	16.5	60	28.5
	5	35	59	240	12	10	31
	6	285	31	255	28.5	170	45

4.4.2 Raw data for the diurnal foraging behaviour experiment during **winter** (10/1/95).

Behaviour:		*None*		*None*		*Open*	
Time:	**No.**	**Bearing**	**Distance**	**Bearing**	**Distance**	**Bearing**	**Distance**
07:30	**1**	70	46	250	62	0	53
	2	20	43	270	55	350	46
	3	340	63	280	53	290	48
	4	330	67	290	52	290	77
	5	270	54	300	62	270	73
	6	250	39	310	73	260	92
08:30	**1**	80	44	240	65	10	52
	2	20	42	270	55	340	44
	3	0	64	280	56	290	47
	4	350	67	290	54	300	74
	5	290	56	300	64	280	74
	6	270	40	310	73	270	95
09:30	**1**	80	42	240	72	0	53
	2	10	44	270	57	340	44
	3	60	64	280	56	290	47
	4	350	67	290	58	290	74
	5	300	54	300	67	280	74
	6	260	38	310	77	280	99
10:30	**1**	80	46	230	80	0	53
	2	10	44	270	58	340	45
	3	0	65	280	56	290	46
	4	340	68	290	57	290	74
	5	300	55	300	66	280	73
	6	270	39	310	80	280	98
11:30	**1**	90	45	220	80	350	52
	2	20	44	270	58	330	46
	3	0	65	280	57	290	48
	4	340	69	290	57	290	74
	5	300	54	300	66	280	74
	6	260	36	320	77	280	99

4.4.2 (contd.)

Behaviour:		***None***		***None***		***Open***	
Time:	**No.**	**Bearing**	**Distance**	**Bearing**	**Distance**	**Bearing**	**Distance**
12:30	**1**	80	37	220	80	350	52
	2	20	45	270	58	330	46
	3	0	64	280	57	290	48
	4	340	68	290	57	290	74
	5	300	54	290	67	280	74
	6	260	36	330	93	280	99
13:30	**1**	110	60	220	85	350	52
	2	20	44	270	58	340	46
	3	0	65	280	57	290	48
	4	350	70	290	57	290	74
	5	300	54	290	67	280	74
	6	260	36	320	98	280	99
14:30	**1**	90	67	230	93	340	57
	2	20	42	270	57	340	46
	3	0	65	280	57	290	48
	4	350	70	300	63	290	73
	5	300	54	290	68	280	74
	6	260	36	340	68	280	100
15:30	**1**	100	49	230	82	340	65
	2	10	42	270	55	340	46
	3	0	65	280	51	290	48
	4	350	70	280	63	290	76
	5	300	54	300	75	280	74
	6	240	35	330	108	280	103
16:30	**1**	80	70	220	63	350	75
	2	10	42	280	56	350	40
	3	0	65	290	55	290	48
	4	350	70	270	66	290	83
	5	300	54	330	99	280	74
	6	240	35	330	108	280	97

Appendix 4.5 Agonistic behaviour

4.5.1 Raw data for the agonistic behaviour experiment during **summer** (18/8/94).

Date 18/8/94	**B. Type** *closed* **Start**	**Finish**	**B. Type** *open* **Start**	**Finish**	**B. Type** *none* **Start**	**Finish**
1	07:11 NF	07:30 IL	07:12 NF	07:32 CE	07:35 NF	07:55 CE
2	07:11 F	07:20 IL	07:12 NF	07:32 CE	07:35 NF	07:45 CB
3	08:01 F	08:16 IL	07:12 NF	07:32 CE	07:35 NF	07:34 CB
4	08:01 F	08:12 IL	07:33 F	07:53 CE	08:04 NF	08:15 CB
5	08:01 F	08:17 IL	07:33 F	07:53 CE	08:04 NF	08:24 CE

4.5.2 Raw data for the agonistic behaviour experiment during **winter** (11/1/95).

Date 11/1/95	**B. Type** *closed* **Start**	**Finish**	**B. Type** *open* **Start**	**Finish**	**B. Type** *none* **Start**	**Finish**
1	07:35 NF	07:38 IL	07:56 NF	08:07 CB	07:20 NF	07:40 CE
2	07:35 F	07:40 IL	07:56 NF	07:58 CB	07:20 NF	07:23 CE
3	07:35 F	07:44 IL	07:56 F	08:02 IL	07:20 NF	07:40 CE
4	07:35 F	07:53 IL	07:56 NF	08:16 CE	07:20 NF	07:32 CB
5	07:35 F	07:55 IL	07:56 F	08:16 CE	07:20 NF	07:40 CE